Determining the role of plant-parasitic nematodes in the crop rotation yield effect, and the influence of crop rotation and nematicide application on the nematode community

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Abstract

In the Midwestern United States, corn-soybean rotation is an essential agricultural practice to increase crop yield, often known as the rotation effect. Plant-parasitic nematodes, particularly soybean cyst nematode (SCN, *Heterodera glycines*) in soybean and *Pratylenchus* in corn, may contribute to the rotation effect and the nematode community is a sensitive indicator of changes in soil ecology. A long-term research site in Waseca, Minnesota was established in 1982 to study corn-soybean rotation. At the site, various corn-soybean crop sequences can be compared each year including corn and soybean in 1 to 5 years of monoculture, annual rotation of each crop, and continuous monoculture of each crop. Granular nematicides (terbufos or aldicarb) have been applied to half of each plot since 2010 to minimize nematode populations across crop sequences. If successful, the rotation yield effect could be compared with unaltered nematode populations and with minimal nematode populations to determine the role of nematodes in the rotation effect. For this thesis, crop yield and plant-parasitic nematode populations were measured from 2010-14 while the nematode community was assessed from 2013-14 at the long-term rotation research site. Specifically, the objectives of this research were to: (i) investigate the impact of crop sequences and nematicide application on plant-parasitic nematode populations and crop yield (Chapter 2), (ii) determine the role of plant-parasitic nematode populations in the corn-soybean rotation effect using nematicide application (Chapter 2), and (iii) study the impact of crop sequences and nematicide application on soil ecology based on the nematode community (Chapter 3). Research related to these objectives is reviewed in Chapter 1.

SCN egg population densities significantly increased in soybean and decreased in corn—particularly in the initial 3 years of monoculture-- so populations were significantly greater in soybean than corn monoculture for most sequences ($P \leq 0.05$, Fischer's LSD). After two to three years of corn monoculture, SCN populations were below 200 eggs/100 cm^3 soil, the proposed damage threshold guideline for SCN, in most seasons. *Pratylenchus* populations significantly decreased in soybean monoculture and increased in corn monoculture—particularly in the initial 3 years of monoculture-- leading to significantly greater *Pratylenchus* populations under corn than soybean monoculture for most sequences ($P \leq 0.05$, Fischer's LSD). *Helicotylenchus* population densities were similar among many crop sequences, but significantly greater in extended corn monoculture and smaller in extended soybean monoculture than most sequences ($P \leq 0.05$, Fischer's LSD). *Xiphinema* was present at the site, but population densities were small at an average of 8 nematodes/100 cm^3 soil across plots and seasons. Corn yields decreased significantly in monoculture, particularly in the initial 3 years in monoculture

($P \leq 0.05$, Fischer's LSD). Soybean yields also decreased significantly in monoculture, often decreasing throughout the length of monoculture tested when comparing crop sequence treatments within single years ($P \leq 0.05$, Fischer's LSD).

Aldicarb nematicide consistently significantly decreased *Pratylenchus, Helicotylenchus*, and *Xiphinema* populations but was inconsistent against SCN ($P \leq 0.05$, ANOVA). Aldicarb nematicide consistently increased corn yield and decreased *Pratylenchus* and *Helicotylenchus* populations ($P \leq 0.05$, ANOVA), suggesting these nematodes, particularly *Pratylenchus*, may have decreased corn yield. Aldicarb nematicide also significantly increased soybean yield in 2012 and 2013, but decreased SCN populations did not consistently correspond with increased soybean yield ($P \leq 0.05$, ANOVA). While nematicide reduced nematode populations, there was still significant variation across crop sequences in most seasons ($P \leq 0.05$, ANOVA), so nematicide application was not a successful method for determining the role of nematodes in the rotation effect in most seasons. However, the strong influence of crop sequences on SCN and *Pratylenchus* populations suggest nematodes have a role in the rotation effect.

Nematicide application also impacted non-target nematodes and thus soil ecology with significantly decreased fungivore and bacterivore populations, diversity, and maturity; but significantly increased enrichment ($P \leq 0.05$, ANOVA). The nematode community and soil ecology was significantly different in corn compared to soybean cropping systems and changed most during initial years of crop monoculture ($P \leq 0.05$, Fischer's LSD). Cropping systems in corn supported significantly greater fungivore populations, fungal decomposition pathways, more diversity, and a more mature ecosystem compared to soybean systems ($P \leq 0.05$, Fischer's LSD). Soybean systems supported significantly greater bacterivore populations and a more disturbed, enriched ecosystem ($P \leq 0.05$, Fischer's LSD). These differences between corn and soybean systems suggest nutrient mineralization by nematodes and other microorganisms may play a role in the benefits of crop rotation for plant growth.

Table of contents

List of tables

Chapter 1

Chapter 2

Chapter 3

Chapter 1: Literature Review

1. Introduction

The research described in this dissertation was conducted at a unique long-term crop rotation site where various sequences of corn (*Zea mays*) and soybean (*Glycine max*) have been established in plots for over 30 years. The goals of this research were to better understand the relationships among crop rotation, crop yield, and soil ecology based on the nematode community. While crop rotation is an ancient technique for increasing the yield of crops, sometimes known as the rotation effect, there is still much to be learned about how crop rotation works. Therefore, the objectives of this dissertation research were to: (1) Assess the influence of long-term corn-soybean sequences on crop yield, (2) Assess the role of plant-parasitic nematodes in this rotation effect, (3) Determine how long-term corn-soybean sequences influence the soil ecosystem as indicated by the nematode community.

Objectives 1 and 2 will be discussed in Chapter 2 while Objective 3 will be discussed in Chapter 3. In Chapter 1, germane research on crop rotations-particularly corn and soybean-- and nematodes will be reviewed. First, research on agronomic factors involved in the rotation effect will be reviewed with strong emphasis on corn and soybean rotations. Second, research on crop rotation's influence on plant-parasitic nematodes and the latter's subsequent influence on the rotation effect will be reviewed with emphasis on the major plant-parasitic nematodes of corn and soybean present at the site of this dissertation research including *Heterodera glycines* (soybean cyst nematode), *Pratylenchus* (lesion nematode), and *Helicotylenchus* (spiral nematode). Last, how the nematode community serves as a bioindicator of the soil ecosystem and the influence of crop rotation on the nematode community will be reviewed.

2. Agronomic factors in crop rotation

Crop rotations are still an integral part of many modern agronomic systems. In the Midwestern United States, corn and soybean are the most important crops and thus the rotation of these crops is well-studied. There is a large body of evidence that rotating corn with soybean increases yield (the rotation effect) while growing corn or soybean in monoculture results in declining yields (monoculture yield decline) (Crookston and Kurle, 1989; Crookston et al., 1991; Meese et al., 1991; Whiting and Crookston, 1993; Porter et al., 1997; Porter et al., 2001; Chen et al., 2001c; Pedersen and Lauer, 2004).

2.1 Soil nutrients influence crop rotation

The primary recognized benefit of corn-soybean rotations is maintaining good soil nutrient levels (Peterson and Varvel, 1989b; Meese et al., 1991; Omay et al., 1998). In particular, rotation with soybean and other nitrogen-fixing legumes increases soil nitrogen levels which contributes to increased yield of corn, which is dependent on adequate soil nitrogen (Peterson and Varvel, 1989b; Meese et al., 1991; Omay et al., 1998). Some studies show that nitrogen is an important factor for the rotation yield effect for corn. At a long-term corn and soybean rotation site in Arlington, Wisconsin, increased nitrogen fertilizer application (224 compared to 112 kg N/ha) corrected monoculture yield decline to a large extent (Meese et al., 1991). Similarly, ten-year monoculture corn supplemented with up to 155 kg N/ha equaled yield of corn in annual rotation in a Kansas study (Omay et al., 1998), and in some years of a Nebraska study, heavy nitrogen application (180 kg/ha) eliminated differences between annually rotated and 12-year corn monoculture (Peterson and Varvel, 1989b).

2.2 Soil nutrients not sole factor in rotation effect

Other research suggests that nitrogen is not the only factor in the rotation effect for corn. Corn has benefited from rotation with non-legumes including sorghum (Robinson, 1966), oats (Bolton et al., 1976), hay (Barber, 1972), and a soybean cultivar incapable of fixing nitrogen (Maloney et al., 1999) that would not benefit soil nitrogen levels like legume crops. Additionally, soil nitrogen is generally not a limiting factor for soybean (Salvagiotti et al., 2008), yet rotation benefits soybean yield also (Meese et al., 1991; Crookston et al., 1991; Porter et al., 1997; Wilhelm and Wortmann, 2004).

A number of studies have also demonstrated that soil nutrients are not the only factor in the rotation effect for corn-soybean systems by documenting the rotation effect even when sufficient soil nutrients are supplied. A primary documentation of this in the Midwest is the long-term rotation (LTR) site at Waseca, MN studied in this dissertation along with partner sites in Lamberton, MN and Arlington, WI which were established in 1982, 1981, and 1983 respectively (Crookston et al., 1991; Meese et al., 1991; Porter et al., 1997). The crop sequence treatments at these sites included both soybean and corn in 1 to 5 years of monoculture, continuous monoculture of each crop, and annual rotation of the two crops. These sites were managed for optimum production particularly such that soil nutrients were not limiting, except in cases where treatments were applied to portions of sites to test specific hypotheses. Soybean cyst nematode (SCN) was not

present at the sites at the beginning of the study, but was present in some plots at the Minnesota sites by 1989 (Porter et al., 2001). A number of reports document the rotation effect at these sites and suggest additional factors that may contribute to the rotation effect.

The first of these reports demonstrated the rotation effect at the Waseca and Lamberton sites 5-9 years after establishment (Crookston et al., 1991). Corn yield was highest in first-year corn that was rotated with five years of soybean (15% better than monoculture) followed by annual rotation (10% yield advantage), with three or more years of monoculture similar, and second-year corn lowest. Soybean had highest yield under first-year soybean (17% yield advantage) followed by annual rotation and second-year soybean (8% yield advantage) and yield gradually declined with increasing years of monoculture except a slight increase with fifth-year soybean. This clearly demonstrated rotation effect for both soybean and corn when nutrients were not limiting suggesting other factors contribute to this phenomenon. Additionally, it suggested for corn yield advantage of rotation is largely erased with consecutive years of corn, but for soybean yield some rotation benefits linger over multiple years.

A second report examined tillage, cultivar, and fertilizer (discussed above) effects within the crop rotations at the long-term site in Arlington, WI over a three-year period from 1987-1989 (Meese et al., 1991). In contrast to the Minnesota results, corn yields were highest in either first year corn sequence and generally decreased with increasing years of corn monoculture. However, overall trend in soybean yields was similar to the previous study with yields generally decreasing with increasing years in monoculture and soybean yields greater following a long than short length of corn production. Extent of monoculture yield decline also varied by corn cultivar and soybean yield under monoculuture was diminished under brown stem rot (causal agent *Phialophora gregata*) susceptible compared to resistant soybean cultivar. This suggests disease pressure and cultivar characteristics played a role in the rotation effect although similar experiments with brown stem rot soybean cultivars at the Minnesota long-term rotation sites suggested root pathogens did not play a large role in the rotation effect (Whiting and Crookston, 1993). In some cases, yield decline under monoculture was greater under no-till than tillage systems suggesting cropping environment influenced rotation effect with residue build-up and compaction possible factors (Meese et al., 1991).

Later, yield was reported across all three long-term rotation sites, from plots managed for optimum production, for a period of 9-11 years—depending on the site--ending in 1995 (Porter et al., 1997). Averaged over years and sites, corn yield was greatest in the first year grown—following either 1 year or 5 years of soybean— with yield increases around 15% compared to continuous corn. Any corn in two or more years monoculture had similar yield. The plateau in yield after two years of monoculture was similar to shorter-term Minnesota results (Crookston et al., 1991), but dissimilar to earlier results at Arlington (Meese et al., 1991). This difference in results may be partially due to the suboptimum nitrogen treatment included in early Arlington results as incremental decreases in soil N levels under that treatment may have incrementally decreased overall corn yield (Meese et al., 1991). Soybean yield in the Porter et al. (1997) study followed a similar trend to other two reports with yield greatest under 1st-year soybean (18% greater than continuous soybean) and decreasing incrementally through third-year soybean and plateauing thereafter. This suggests, over a range of Midwestern growing conditions, on average, yield advantage of rotation for corn lasts only one year while yield advantage, or yield decline, lingers over 3 years of monoculture for soybean. Yield advantage of rotation was also greater in low-yielding environments (years at specific locations where conditions were not conducive to crop growth) which is in agreement with specific observations at Arlington under disease pressure, with limited N availability, and potentially stressful no-tillage practices (Meese et al., 1991). Together, these studies demonstrated that factors other that soil nutrients contribute to yield increase with soybean-corn rotation in the Midwest.

Other long-term studies have also demonstrated this. A study established for 16 years near Lincoln, Nebraska also showed both corn and soybean yields were increased under annual rotation compared to continuous monoculture even when necessary nutrients were supplied (Wilhelm and Wortmann, 2004). This study also suggested rotation had greater benefit to corn under cool conditions, but that soybean rotation benefits were unaffected by environment and tillage type did not affect benefits of rotation for either crop. In a study of corn and soybean monoculture and annual rotation established for 7 years in Tennesse under no-till conditions with N supplied at 168 kg N/ha, PK fertilization did not correct monoculture yield decline (Howard et al., 1998).

2.3 Other agronomic factors in rotation effect

In other research, specific factors other than soil nutrients that may contribute to the rotation effect have been identified. In a study of limited treatments (first and fourth-year crops only) at the previously mentioned long-term rotation site at Lamberton, in 1991-1992, root growth was affected by cropping sequence albeit differently for each crop (Nickel et al., 1995). First-year corn following 5 years of soybean had more dense root systems than fourth-year corn at soil depths 12-37.5 cm from the middle of the season onward. However, fourth-year corn root density was greater at 0-12 cm early in the season. The authors (Nickel et al., 1995) suggested corn root growth in monoculture was restricted in lower soil layers by autotoxins, plant compounds toxic to the same crop, from previous corn which leached below the upper soil layer. Alternatively, residue build-up and other factors could have increased compaction in corn monoculture restricting root growth as suggested by studies showing corn-soybean rotation benefits are more pronounced under no-till systems, particularly for corn (Dick and Vandoren, 1985; Griffith et al., 1988; Meese et al., 1991). In contrast, soybean root density tended to be greater under fourth-year than first-year soybean except for soil samples at 37.5-50 cm depth when the trend was reversed. The authors note that soybean roots tend to follow channels made by previous root systems although this does not fully explain the trend in soybean root density. In summary, the study suggested decrease in corn root growth under monoculture may have contributed to yield decline, but that soybean root growth did not (Nickel et al., 1995).

Other studies have further examined the role of crop residues in the rotation effect. In a 3 year study at Lamberton and Waseca, Minnesota, treatments including crops of corn, corn with triacontanol application (a chemical in soybean residue), fallow, and soybean were applied in year 2 while corn was grown in years 1 and 3. Final corn yield was greatest when rotated with soybean crop or fallow and least in corn monoculture with or without triacontanol (Crookston et al., 1988). Since either rotation increased yield, the authors conclude that yield increase was due to alleviation of negative autotoxic chemicals in corn rather than beneficial substances in soybean residue which argees with conclusions of Nickel (1995). However, neither tested for autotoxic compounds in corn residue or manipulated corn residue, so alternate explanations are possible.

A study at multiple Minnesota sites did study the influence of residue management (retension or removal) crossed with previous crop (corn or soybean) on

both soybean and corn yield for one rotation cycle (Crookston and Kurle, 1989). While crop rotation increased both corn and soybean yields, residue removal or addition did not affect yield suggesting stimulatory or inhibitory compounds or other factors associated with shoot residue did not influence the rotation effect. This lead the authors to conclude that negative physical or chemical properties of root residue contributed to monoculture yield decline since soil nutrients were managed for optimum plant growth (Crookston and Kurle, 1989). In a corn seedling bioassay, corn shoot residue extract inhibited corn seedling growth, particularly when extract was incubated in water but also when incubated in soil, (Yakle and Cruse, 1984). This suggests corn residue contains autotoxins as also proposed elsewhere (Crookston et al., 1988; Nickel et al., 1995; Pikul et al., 2012). However after 30 days of incubation in soil, the residue extracts did not inhibit corn growth possibly because any autotoxins were decomposed by microbes (Yakle and Cruse, 1984). This short-term duration make it unlikely autotoxins in corn shoot residue would affect subsequent crop growth.

Other studies at the Minnesota LTR sites have also connected changes in crop physiology to the rotation effect. At the Waseca and Lamberton sites; N, P, and K concentration and total accumulation in corn shoots were greater in first-year than continuous monoculture despite adequate soil nutrient levels (Copeland and Crookston, 1992). However, nutrient concentration and accumulation in soybean shoots was generally not affected by rotation with exceptions being increased P concentration and accumulation at early vegetative stage and increased K concentration at early vegetative and reproductive stages. This showed that corn nutrient status was affected by rotation independent of soil nutrient status and is supported by a South Dakota study that demonstrated greater nitrogen use efficiency for rotated than monoculture corn (Pikul et al., 2012). Reduced shoot nutrient levels under corn monoculture may be due to the observed decrease in root density (Nickel et al., 1995) or other means such as decreased nutrient uptake efficiency by roots, translocation to shoots, or nutrient transportation through soil. In contrast, any differences in soybean root density (Nickel et al., 1995) did not appear to affect soybean nutrient accumulation (Copeland and Crookston, 1992).

Soil moisture and water use by crops has also been associated with the rotation effect. At the Minnesota long-term rotation sites in 1987 and 1988, crop rotation influenced water use by crops (Copeland et al., 1993). First-year corn depleted more

water from the soil and had more evapotranspiration over a single growing season than continuous corn. This is consistent with the increase in root density also observed at the Lamberton site for a different time period (Nickel et al., 1995) which would increase water uptake capacity. Similar to previous reports, corn yield was also greater for 1st-year corn, so water use efficiency (yield/evapotranspiration) did not differ among rotations (Copeland et al., 1993). This raises the question of whether decreased water uptake by corn contributed to decreased corn yield or decreased water uptake was merely a byproduct of decreased corn yield. In contrast, in a South Dakota rotation study, soil moisture generally did not differ between corn monoculture and annual rotation over the first eight years of the study (Pikul et al., 2012) or between annual rotation and corn monoculture in a Nebraska study (Peterson and Varvel, 1989b). In the South Dakota study, since rotation effect was observed, water use efficiencies were greater for annually rotated than monoculture corn (Pikul et al., 2012). Similar to previous studies, yield advantage of rotation was also greater in dry, low-yielding years.

At the Minnesota long-term rotation sites, soil water depletion did not differ among soybean rotations, but water use efficiency did since yield was higher for 1st-year than monoculture soybeans (Copeland et al., 1993) with similar trends in the previously discussed South Dakota study (Peterson and Varvel, 1989a). Water demands were greater for corn than soybean and water table recharged over winter season even in dry years, so crop rotation influenced only in-season not long-term soil water dynamics (Copeland et al., 1993).

Similarly, in a study on soybean-sorghum crop sequences, soil moisture was greater in sorghum than soybean and, to a lesser extent, in continuous monoculture than annual rotation for either crop over three growing seasons seven years after establishing rotations (Roder et al., 1989). Crops in rotation yielded better than in monoculture which may have contributed to moisture differences, similar to trends in corn-soybean rotation (Copeland et al., 1993), although this does not account for early-season differences in soil moisture. In one spring before planting, previous crop influenced water content with soil drier when soybean was the previous crop. The authors suggest greater amount of residue to hold in water under sorghum and differences in water infiltration under different cropping system, as demonstrated elsewhere (Fahad et al., 1982), are responsible for these differences. Unlike other results (Copeland et al., 1993), this suggests some cropping systems can influence soil moisture across growing seasons.

Experiments at the Arlington long-term rotation site showed that soil moisture was greater under 1st-year soybean that followed 5 years corn than soybean in annual rotation or any length of monoculture (Pedersen and Lauer, 2004). Soybean was also taller in 1st or 2nd year of either rotation than with three or more years of monoculture showing rotation influenced soybean development. The authors suggested soil moisture was decreased under soybean monoculture due to decreased crop residue to hold in moisture and promote water infiltration. Elevated soil moisture under corn monoculture observed at Minnesota LTR sites (Copeland et al., 1993) supports this hypothesis as 1st-year soybean at the Arlington LTR followed corn monoculture. Increased soil moisture under sorghum compared to soybean—which produces less residue--also supports this (Roder et al., 1989). However, decreased soil moisture under 1st-year soybean following the high-residue sorghum does not fit this model (Roder et al., 1989) nor does similarity in soil moisture among rotations for soybean at the Minnesota long-term rotation sites (Copeland et al., 1993). In summary, these studies show crop rotation can influence soil moisture and suggest factors including amount of residue and crop uptake of water may be involved. In some cases, soil moisture was related to crop yield although it was unclear if soil moisture influenced or was a result of differences in crop yield.

Based on these studies, soil nutrients play a large role in the rotation effect, particularly for corn, but do not account for the entire effect. Other agronomic factors including soil moisture, soil structure, amount of crop residue, and crop residue physical or chemical properties seem to influence or contribute to the rotation effect but the role of each is not fully determined.

3.1 Pathogens, pests, plant-parasitic nematodes and crop rotation

Other factors often associated with corn-soybean rotation and the rotation effect are pathogen and insect pest populations that reside or overwinter in soil. Studies in southwestern Ontario and Quebec have demonstrated crop rotation with corn or winter wheat decreases *Sclerotinia sclerotiorum* population compared to soybean monoculture (Gracia-Garza et al., 2002; Rousseau et al., 2007). Corn-soybean rotation decreased anthracnose leaf blight (*Colletotrichum graminicola*) incidence and increased yield compared with corn monoculture in a Wisconsin study (Jirak-Peterson and Esker, 2011). In another study in Wisconsin, soybean monoculture increased incidence of *Diaporthe phaseolorum*, var. *sojae* infection of plants compared with rotation including corn, and this pathogen was strongly negatively correlated with soybean yield (Pedersen and

Grau, 2010). Rotation with soybean has been used to manage western corn rootworm (*Diabrotica virgifera*, Coleoptera: Chrysomelidae) in corn (Chu et al., 2013).

In corn-soybean cropping systems, plant-parasitic nematodes can be the main disease pressure, crop rotation is a major practice for managing these nematodes, and plant-parasitic nematodes may have a role in the rotation effect. A successful rotation for nematode management alternates a host crop or crops with a non-host crop or crops for a certain period, and, during the non-host period, the nematode population decreases alleviating stress on host crops. The natural mortality of nematodes continues during the non-host period (Chen et al., 2001c; Belair et al., 2002), perhaps enchanced by starvation of some nematode stages, but is not balanced by reproduction because plant-parasitic nematodes cannot complete their life cycle without a host (Belair et al., 2002; Belair et al., 2007; Warnke et al., 2008). Nematode population mortality and rate of decline will be affected by environmental conditions such as temperature, moisture, and soil properties with more extreme conditions decreasing nematode viability which will vary by species (Townshend, 1971; Hamblen et al., 1972; Goodell and Ferris, 1989; MacGuidwin and Forge, 1991; Yen et al., 1995; Riggs et al., 2001). Nematodes with fewer adaptations for surviving harsh conditions--such as nematodes that do not form cysts--will have decreased viability compared to adapted nematodes (Inagaki and Tsutsumi, 1971). Nematodes that hatch in the absence of a host, such as *Meloidogyne* (Goodell and Ferris, 1989; Wesemael et al., 2006), will have lower viability than nematodes stimulated to hatch by host signals such as *Heterodera* (Warnke et al., 2008) as most hatched nematodes will not survive for long in the absence of a host (Goodell and Ferris, 1989).

Planting of certain crops can also accelerate nematode decline, particularly trap crops, nematotoxic crops, and green manure crops (Oka, 2010). Trap crops stimulate nematode hatch, but are poor hosts that the particular nematode cannot develop on leading to increased nematode death rates (Chen et al., 2001a; Smith et al., 2004; Hafez and Sundararaj, 2009). Nematotoxic crops contain compounds that kill or impair nematodes reducing nematode population immediately or gradually over time (Warnke et al., 2008; Szakiel et al., 2008; Zasada et al., 2009; Gimsing and Kirkegaard, 2009; Oka, 2010; Doligalska et al., 2011). Green manure crops can stimulate microbial antagonists of plant-parasitic nematodes contributing to decline of these nematodes (Matthiessen and Kirkegaard, 2006; Oka, 2010) in addition to any trapping or

nematotoxic effects. Co-occurrence of multiple plant-parasitic nematode populations complicates outcomes of rotation as competition may occur between nematodes or rotation may adequately manage only certain nematodes present (Lawn and Noel, 1986; Melakeberhan and Dey, 2003).

In production settings, the necessary length of non-host cropping may vary from one season to many years depending on factors such as initial nematode population density, nematode pathogenicity, rate of nematode decline, environmental conditions, crop, desired level of nematode control, and other management strategies employed (Windham, 1998; Kinloch, 1998; Porter et al., 2001; Chen et al., 2001c). Crop rotation is generally integrated with other strategies including use of resistant cultivars, nematicide, biocontrol, and cultural practices to manage plant-parasitic nematodes.

In Midwestern corn-soybean rotations, SCN is the primary nematode of concern in soybean while various nematodes can cause problems in corn including *Pratylenchus*, *Helicotylenchus,Tylenchorhynchus, Beloinolaimus*, *Xiphinema*, or *Longidorus* (Windham, 1998; Kinloch, 1998). In the following, management of SCN, *Pratylenchus*, and *Helicotylenchus* by crop rotation and evidence of the role of these nematodes in the rotation effect are discussed as they were the major nematodes of concern for this dissertation research.

3.1 Soybean cyst nematode and crop rotation

The soybean cyst nematode is the major yield-limiting pathogen of soybean in the United States, causing an estimated 3 million Mg of soybean yield loss in 2009, representing one quarter of the total yield loss to diseases (Koenning and Wrather, 2010). SCN juveniles and females feed on soybean roots by inducing formation of a syncytium-a feeding site of a large, multinucleated soybean cell (Noel, 2004). This feeding induces damge with symptoms including stunted, chlorotic shoots; stunted roots with reduced ability to uptake water and nutrients; and yield loss. SCN generation time is around 30 days in the field, so the nematode population has three to four generations to increase during a Midwestern growing season. The SCN overwintering structure is the cyst, the dead, hardened female body which protects enclosed eggs from environmental pressures allowing eggs to survive for ten years or more and hatch when conditions are favorable (Inagaki and Tsutsumi, 1971).

Use of resistant soybean cultivars is a major SCN management strategy in the Midwest. Resistant cultivars will not form a functional syncytium preventing SCN feeding

on soybean roots (Koenning, 2004). Resistant cultivars have been effective for decreasing SCN populations while increasing soybean yields in Minnesota with yield increases of 28% in some cases (Chen et al., 2001b; Chen et al., 2001c; Chen et al., 2007). Continuing efficacy of this strategy is a concern as nematode populations are adapting to overcome the few commercially available sources of SCN resistance (Schmitt et al., 2004; Zheng et al., 2006; Kim et al., 2011).

Crop rotation is the other major SCN management strategy in the Midwest. When soybean is rotated with non-host or poor host crops, SCN population is reduced minimizing soybean yield loss in subsequent years (Porter et al., 2001; Chen et al., 2001c). In northern regions, non-host crop rotation alone is generally not effective for controlling SCN, but is used in combination with SCN-resistant soybean cultivars (Chen, 2011). Extensive work has been done to catalog hosts, non-hosts, and poor hosts of SCN (Porter et al., 2001; Chen et al., 2006; Warnke et al., 2006; Warnke et al., 2008). Some known non-host or poor host crops commonly grown in Minnesota include corn, perennial ryegrass, canola, red clover, oats, wheat, pea, clover, alfalfa, sugar beet, sunflower, and barley (Riggs and Hamblen, 1966; Riggs, 1987; Sortland and MacDonald, 1987; Warnke et al., 2006).

A field study at various sites in Minnesota showed barley, flax, oat, sorghum, wheat, canola, corn, potato, sunflower, alfalfa, hairy vetch, red clover, and pea can reduce in-season SCN population growth compared to susceptible soybean, although amount and consistency of the reduction varied (Miller et al., 2006). These one year rotations did not generally affect susceptible soybean yield or SCN populations in the following year suggesting longer rotations or additional strategies are needed for effective management (Miller et al., 2006).

In greenhouse studies, various potential rotation crops reduced SCN population including sunn hemp (*Crotalaria juncea*), forage pea (*Pisum sativum*), lab-lab bean (*Lablab purpureus*), Illinois bundleflower (*Desmanthus illinoensis*), and alfalfa (*Medicago sativa*) (Warnke et al., 2006). Additional greenhouse studies showed residues of sunn hemp, red clover, and perennial ryegrass incorporated in fallow soil can reduce SCN egg population and subsequent infectivity. *In vitro* studies showed the extracts of fresh plants or plant residue from sunn hemp, red clover, soybean, and canola can reduce viability of SCN J2 (Warnke et al., 2008).

Corn is the primary crop rotated with soybean in the Midwestern United States due to its economic importance and suitability for growth in this region. Therefore, the impact of corn-soybean rotations on SCN population dynamics and crop yield is well-studied. One study over 4 years in Waseca and Lamberton, Minnesota compared SCN populations under various crop sequences: monoculture of corn, SCN-susceptible soybean or SCN-resistant soybean; rotation of susceptible soybean with 1 to 3 years of corn; resistant soybean-corn annual rotation; and soybean-corn annual rotation alternating resistant and susceptible in the soybean phase (Chen et al., 2001c). Rotation with corn effectively reduced SCN populations, but not below threshold levels quickly enough to manage SCN on its own. Within single growing seasons, SCN populations were reduced between 24 and 77% under corn, between 27 and 79% under resistant soybean, and increased between 1.76 and 9.91 times under susceptible soybean. Corn to SCN-resistant soybean annual rotation or corn monoculture minimized SCN population and SCN populations decreased as years in corn increased. Susceptible soybean yield was greater following corn and soybean yields were negatively correlated with SCN populations in some cases suggesting SCN had role in yield benefits of crop rotation. However, yield was not always significantly correlated with SCN yield, suggesting other factors also influenced soybean yield.

Influence of initial nematode population and site characteristics on nematode management with crop rotation was clearly demonstrated by differences in SCN population dynamics at the Waseca site (initially 6,800 eggs/100 cm^3 soil) compared to the Lamberton site (15,095 eggs/100 cm^3 soil). After 4 years of growing corn, SCN population density was 400 eggs/100 cm^3 soil at the Waseca site—near the damage threshold of 200 eggs/100 cm^3 soil—compared to 1,500 for the same sequence at the Lamberton site demonstrating the longer time growing non-host crop needed at higher initial populations. This demonstrates long rotations--over four years of non-host—are needed at some Midwest sites to reduce SCN population below damage threshold for SCN-susceptible soybean making crop rotation alone an inefficient management strategy (Chen et al., 2001c). SCN biology, including long-term survival in cysts (Noel, 2004) and limited hatch in the absence of hosts (Warnke et al., 2006), contribute to this slow decline of SCN populations.

Influence of crop sequence on SCN population at the long-term rotation sites in Waseca and Lamberton were reported for 1996-98, well after SCN was initially detected

at the sites in 1989 (Porter et al., 2001). SCN populations increased rapidly when soybean was grown, generally reaching the statistical maximum observed in the study by the end of the second year soybean was grown (around 4,000 and 8,000 eggs/100 cm^3 soil at Waseca and Lamberton respectively) suggesting benefits of crop rotation do not last long into host monoculture cycles, even following five years of non-host cropping. Similarly, SCN population decreased rapidly when corn was grown, particularly at the Lamberton site where density was around 500 eggs/100 cm^3 soil by the end of the first year in corn. For both sites, by the 3rd year in corn, SCN was barely detectable. This contrasts with the study at other Minnesota sites (Chen et al., 2001c) where SCN declined gradually and remained at damaging levels after four years of non-host corn. Again, this shows SCN population dynamics are, to some degree, dependent on site and environmental conditions.

Rotation with 5 years of corn was better than annual rotation for managing SCN population and annual rotation managed initial SCN density before soybean crop better than soybean monoculture of two or more years (Porter et al., 2001; Pedersen and Grau, 2010). Similarly, soybean yields were greatest under first-year soybean following five years corn (Lamberton) or similar to annual rotation (Waseca). After 2nd year of soybean, yields generally decreased gradually with increasing years in soybean at the Lamberton site, but remained relatively constant after second year in soybean at the Waseca site. Soybean yields were significantly correlated with final SCN population at Lamberton suggesting SCN had a role in the rotation effect. However, the lack of correlation between SCN and yield at Waseca and differences in SCN population dynamics between sites suggest site-specific biological or physical factors influenced the rotation effect.

In a study at the Arlington, Wisconsin, long-term rotation site and a more recently established Iowa site, yield and SCN population were compared for soybean phases of the LTR crop rotation treatments: annual rotation; 1st, 2nd, or 3rd year soybean following 4 or 5 years corn; or soybean monoculture (24-26 years at Wisconsin or 3-6 years at Iowa) (Conley et al., 2011). Within rotation treatments, plots were split into treatments of SCN-susceptible or resistant cultivars. SCN population was greater with annual rotation than first-year soybean after 4-5 years of corn suggesting longer non-host phase had initial benefits as also demonstrated at Lamberton (Porter et al., 2001). SCN population increase under soybean in this study was similar, albeit somewhat more gradual, to

trends at Minnesota long-term rotation sites (Porter et al., 2001) as population increased steadily over the first three years of soybean and did not reach maximum population in this time (Conley et al., 2011).

Yield was related to SCN population at the Wisconsin sites (Conley et al., 2011), decreasing with increasing years of monoculture similar to trend at Lamberton site (Porter et al., 2001). By the 3rd year of soybean, yield and SCN populations were similar to annual rotation again suggesting even long phases of non-host cropping benefit for only a couple years. At the Iowa site, planting SCN-resistant cultivar evened out yield and SCN population among crop sequences to some degree compared to that with SCN-susceptible soybean, demonstrating SCN has a role in the rotation effect (Conley et al., 2011). However, this was not observed at the Wisconsin site. While these studies suggest SCN has a role in the rotation effect for soybean, other factors influence soybean yield under rotation as rotation effects on yield were observed at the LTR sites before SCN was established there (Crookston et al., 1991; Meese et al., 1991; Copeland and Crookston, 1992; Whiting and Crookston, 1993; Copeland et al., 1993).

In an Illinois field study of initial SCN infestation, SCN-susceptible soybean rotated annually with corn had lower SCN population and higher yield than susceptible soybean monoculture (Noel and Edwards, 1996). In contrast, when SCN-resistant cultivar was used, rotation did not decrease SCN population and yield advantage was rarely observed. This suggests SCN management had a major role in yield advantage for rotated soybean. Additionally, crop rotation delayed but did not prevent the establishment of SCN compared to soybean monoculture in plots inoculated with SCN.

Crop rotation is known to be more effective for managing SCN populations in warmer regions such as the southern United States because SCN overwintering survival is poorer in these regions (Riggs et al., 2001). As a result, SCN populations decrease more rapidly under non-host cropping in warmer regions making rotations with shorter non-host phases more effective than in cooler regions.

This is illustrated by field studies in the southern United States where SCN population was near minimum detectable limits after first year corn in North Carolina (Koenning and Barker, 1995), Louisiana (Dabney et al., 1988), and Tennesse studies (Young, 1998); or by second year of non-host cropping in a North Carolina study (Koenning et al., 1993). In Minnesota, at least three years of corn cropping were needed to reduce SCN to similar levels (Porter et al., 2001).

Studies in the southern United States demonstrate that crop rotation is effective both for reducing SCN population and increasing soybean yield in that region. In a North Carolina field study, annual soybean-corn rotation was beneficial, decreasing SCN population at the end of corn cropping (Koenning and Barker, 1995). Similar to the trend in northern climates (Porter et al., 2001), SCN population increased rapidly when soybean was grown in the North Carolina study (Koenning and Barker, 1995). Population increase was greater following 1 than 2 years of corn though. Rotation effect was observed for soybean yield with yield decreased under monoculture compared to rotation but minimal difference between annual and 3-year rotations (Koenning and Barker, 1995). Similarly, in another North Carolina field study rotation with a non-host crop, including corn, effectively decreased SCN population and increased soybean yield (Koenning et al., 1993). In both of these studies, soybean yield was inversely related to SCN density suggesting SCN had a role in the rotation effect (Koenning et al., 1993; Koenning et al., 1995).

In a Tennesse field study, soybean-soybean-corn rotation decreased final SCN population in corn year and increased soybean yield following corn compared to soybean monoculture suggesting SCN management by rotation may have contributed to yield increase (Young, 1998). In a different Tennesse field study (Howard et al., 1998), annual rotation of corn with SCN-susceptible soybean diminished SCN populations compared to soybean monoculture. Decreased SCN population coincided with increased soybean yield suggesting SCN management by rotation may have contributed to yield increase (Howard et al., 1998).

In another Tennesse field study, SCN population increased more in SCN-resistant soybean monoculture than annual rotation of corn and resistant soybean over eleven years following study establishment (Young and Hartwig, 1992). This suggests rotation delayed SCN adaptation to overcome plant resistance. However, yield was not greater in rotation than monoculture with resistant soybean, so SCN did not influence yield of resistant soybean and other factors did not contribute to rotation effect in this case.

In an Alabama field study, yield was lower in continuous soybean than corn-soybean annual rotation or wheat-soybean rotated with corn. However, SCN population in soybean was greater in continuous or annual rotation soybean than wheat-soybean-corn rotation, so yield and SCN population were not directly related (Edwards et al.,

1988). Yield and SCN population trends were more dramatic under conventional than minimal tillage systems.

In a Louisiana field study, soybean rotation with either fallow or sorghum increased soybean yield and decreased SCN compared to monoculture. When an SCN-resistant soybean was used, yield benefit of rotation was decreased along with SCN populations. Therefore, SCN control was identified as the main contributor to the rotation effect for soybean yield in this study (Dabney et al., 1988). Single year of non-host cropping reduced SCN populations to below 200 cysts/liter.

In summary, crop rotation is one of the main strategies for SCN management, but is generally used in combination with SCN-resistant soybean cultivars. In particular, rotation with corn is an effective and commonly used practice for helping manage SCN populations in Midwestern soybean production. SCN populations increase in soybean monoculture and are known to reduce soybean yield suggesting SCN contributes to monoculture yield decline of soybean in some cases. Additionally, some studies have demonstrated more directly the involvement of SCN in the rotation effect by showing monoculture yield decline is more dramatic in the presence of SCN. However, SCN is only one factor in the rotation effect for soybean as the rotation effect has been observed when SCN is not present (Crookston et al., 1991; Meese et al., 1991; Copeland and Crookston, 1992; Whiting and Crookston, 1993; Copeland et al., 1993).

3.2 *Pratylenchus* and crop rotation

Pratylenchus is an important pest of many crops including both corn and soybean although host range varies by species. *Pratylenchus* are migratory endoparasites that enter the root near the root cap and cause physical damage to cells as they penetrate the roots and induce changes in plant physiology by feeding on plant cells (Windham, 1998). This leads to symptoms including areas of decayed root (lesions), stunted roots, lateral root proliferation, and stunted shoots. *Pratylenchus* can be damaging in a wide range of soil types (Smolik and Evenson, 1987; Niblack, 1992; Todd and Oakley, 1996; Pudasaini et al., 2006; Viaene and Baidya, 2007), although coarser soils may favor infection (Townshend, 1972). *Pratylenchus* have life cycles as short as 3 to 4 weeks on corn (Windham, 1998) so they can build up to high densities in the soil or in plant roots (Todd and Oakley, 1996). Because *Pratylenchus* eggs may be laid inside roots and all life stages feed on or in roots, *Pratylenchus* may have high density in corn or soybean roots while soil density remains low (Schmitt and Noel, 1984;

Windham, 1998). Thus, in corn, damage by *Pratylenchus* may be high even when soil populations are low (Norton, 1984; Windham, 1998; Tylka, 2011). On soybean, *Pratylenchus* is generally not considered a major nematode of concern, partly because SCN is thought to displace other plant-parasitic nematodes in the Midwestern United States (Niblack, 1992).

In the Midwest, *Pratylenchus hexincisus*, *Pratylenchus scriberni*, and *Pratylenchus penetrans* are the most common *Pratylenchus* species in corn fields, but species composition varies from field to field and multiple species may be present in a single field (Windham, 1998). All three species are also common in soybean fields (Schmitt and Noel, 1984) and both corn and soybean are reported to be hosts for all three (Zirakparvar, 1980; Schmitt and Barker, 1981; Todd, 1991; Belair et al., 2002).

Since *Pratylenchus* species have wide host ranges, finding a suitable non-host or poor host crop that effectively reduces nematode population in a crop rotation is challenging. Another factor complicating *Pratylenchus* population management with crop rotation is intraspecific variability in host pathogenicity. Within a *Pratylenchus* species, the range of host plants or cultivars may vary by population making it difficult to predict impacts of a particular crop rotation on *Pratylenchus* population at a given site (Zirakparvar, 1980; Schmitt and Barker, 1981; Todd, 1991; Belair et al., 2002).

The influence of crop rotation on *Pratylenchus* in corn-soybean cropping systems is not well-researched. *Pratylenchus penetrans* can be highly damaging to corn, and is reported to increase on soybean in greenhouse and field conditions (Belair et al., 2002; Chen and Tsay, 2006) and damage soybean in greenhouse conditions (Schmitt and Barker, 1981). Similarly, a greenhouse study suggested *P. hexincisus* reproduces well on both corn and soybean and damages both when in sufficient concentration (Zirakparvar, 1980) although a Missouri study suggested *P. hexincisus* population densities were not related to soybean yield under field conditions (Niblack, 1992). This suggests corn-soybean crop rotation will not be effective for *P. penetrans* or *P. hexincisus* management (Belair et al., 2002).

For *P. scriberni*, crop rotation field studies in addition to host range tests suggest corn-soybean rotation does not effectively manage this nematode. In Florida, double-cropping with first-crop soybean compared to sorghum, both preceding corn, increased *Pratylenchus* populations, mainly *P. scriberni* (McSorley and Gallaher, 1993). Likewise, in a Kansas field study, soil populations of *P. scriberni* were similar for all rotations in

corn (two-year monoculture, annual rotation with soybean or fallow) or soybean (two-year monoculture or annual rotation with corn) (Todd, 1991). Root populations under either soybean rotation were similar to corn in monoculture or corn in annual rotation with fallow. However, soybean in monoculture or annual rotation with corn supported smaller nematode populations in roots than corn in annual rotation with soybean. This suggests that short-term rotation with soybean was not an effective management tool, but that longer-term rotations with soybean may eventually lower *P. scriberni* compared to corn monoculture although further research is need to determine if this decrease would be meaningful for nematode management.

Examples from other cropping systems suggest crop rotation can play a role in *Pratylenchus* management. In Quebec, annual rotation with grain and forage pearl millet reduced *P. penetrans* populations and increased yield in both tobacco (Belair et al., 2004) and potato (Belair et al., 2005; Belair et al., 2006) systems providing viable alternatives to chemical control and previous cropping systems. *Pratylenchus penetrans* populations were reduced and potato yield increased after 2 years oat or 1 year of oat crop in combination with a marigold or *Rudbeckia hirta* cover crop (LaMondia, 2006). Four-year rotation of peanut, cotton, corn, and soybean helped manage mixed populations of *Pratylenchus zeae* and *Pratylenchus brachyrus* in Georgia better than corn or soybean monoculture (Johnson et al., 1975). After 23 years in an Australian long-term system, *Pratylenchus* population was lower under a wheat-lupin annual rotation than wheat monoculture (Rahman et al., 2007).

In summary, the wide host range of *Pratylenchus* populations make management of these nematodes with crop rotation difficult and make it unlikely *Pratylenchus* plays a role in the rotation effect for most cropping systems. However, for systems where a suitable non-host crop can be employed, crop rotation can be used for *Pratylenchus* management. Soybean-corn rotations are unlikely to help manage most *Pratylenchus* populations, particularly species in the Midwestern United States, since both crops serve as hosts for most populations reported. Therefore, management of *Pratylenchus* populations is not expected to play a role in the rotation effect for corn-soybean systems.

3.3 *Helicotylenchus* and crop rotation

Helicotylenchus are medium-sized nematodes that have very wide host ranges and are present in most Midwestern soybean and corn fields (Norton, 1984; Schmitt and

Noel, 1984; Kinloch, 1998; Windham, 1998). *Helicotylenchus dihystera, H. digonicus*, and *H. pseudorobustus* are among the most common species in corn (Norton, 1984; Windham, 1998) with *H. dihystera* and *H. psuedorobustus* especially prolific in soybean (Kinloch, 1998). *Helicotylenchus* are migratory ectoparasites or semi-endoparasites that generally do not penetrate or only partially penetrate the root (Norton, 1984; Windham, 1998). Symptoms of infection include small brownish root lesions (Norton, 1984). They are not considered very pathogenic to corn or soybean, with very high numbers necessary to cause yield loss (Niblack, 1992; Kinloch, 1998; Windham, 1998) although yield increases of 15 to 20% have been reported in nematicide-treated, *Helicotylenchus*-infested corn fields (Norton et al., 1978).

Because they are not considered an important pathogen and have a wide host range, the impact of crop rotation on *Helicotylenchus* is not well-studied. In the previously discussed Georgia rotation study with mixed nematode populations, *H. dihystera* population density increased greatly after four years of soybean monoculture (Johnson et al., 1975). In contrast, corn monoculture only supported small populations of *H. dihystera* suggesting corn was a poor host for this species or that other nematode species outcompeted *H. dihystera*. A corn-soybean-cotton-peanut rotation decreased populations compared to soybean monoculture (Johnson et al., 1975) and in another Georgia field study, four-year rotation including cotton, triticale, and soybean decreased *H. dihystera* populations compared to soybean-triticale annual rotation (Johnson et al., 1998) suggesting some rotations may influence population of this nematode.

In Illinois, *H. pseudorobustus* populations were greater in experimental blocks grown to corn (one or two years) or to soybean that followed corn than soybean following any other crop (Ferris and Bernard, 1971a). Similarly, in another Illinois field study, *H. pseudorobustus* populations did not increase in plots of SCN-susceptible or resistant soybean (Lawn and Noel, 1986). However, in greenhouse experiments, *H. pseudorobustus* reproduced well on soybean (Ferris and Bernard, 1971b; McGawley and Chapman, 1983) suggesting competition from other nematodes may have limited *H. pseudorobustus* population in soybean fields.

In summary, there is some evidence that certain crop sequences may increase *Helicotylenchus* populations and host preference varies by nematode species. For corn-soybean rotations, *H. dihystera* seems to reproduce better in soybean than corn (Johnson et al., 1975) while *H. pseudorobustus* preferred corn to soybean (Ferris and

Bernard, 1971a; Lawn and Noel, 1986). However, all of these field studies had mixed nematode populations with more aggressive nematodes than *Helicotylenchus* present (Ferris and Bernard, 1971a; Johnson et al., 1975; Lawn and Noel, 1986), so these trends may differ depending on nematode species present. Additionally, since *Helicotylenchus* is not known to be very damaging to corn or soybean (Niblack, 1992; Kinloch, 1998; Windham, 1998), influence of crop rotation on this nematode is unlikely to be important in the rotation effect.

4. Soil ecology and nematode community analysis

Increase in beneficial microorganisms or shifts in soil ecology may also contribute to the rotation effect. In experiments at the Lamberton and Waseca long-term rotation sites that focused on continuous and 1st-year corn and soybean, vesicular-arbuscular mycorrhizae (VAM) populations differed by crop for certain species with different species preferring different crops (Johnson et al., 1991). VAM species composition varied by site with detection of cropping preference also varying by site. At the Waseca site, corn seedling root colonization by VAM was slightly greater in continuous than first-year corn. Other studies have suggested increased nutrient mineralization by soil microbes following soybean compared with corn contributes to benefits of corn-soybean rotation for corn (Green and Blackmer, 1995; Gentry et al., 2001). Many aspects of soil ecology under different crop sequences are not well-studied and may hold the key to better understanding crop rotation and the rotation effect.

One prominent measure of soil ecology that is sensitive to many environmental factors is nematode community analysis. Compared to other microbes, nematodes are large and have distinct morphological features, making it relatively easy to distinguish nematode taxonomic groups (Bongers, 1990). Additionally, nematodes span a wide range of trophic groups including herbivores (feed on plants), fungivores (feed on fungi), bacterivores (feed on bacteria), predators (of other invertebrates), and omnivores (combination of food sources), allowing them to be used as indictors of various ecological processes in the soil (Yeates et al., 1993). Due to their range of niches and ability to be counted relatively easily, they can be used to analyze trophic structure and other measures of soil ecology (Bongers and Bongers, 1998).

Nematode community trophic groups and indices are summarized in Table 1.1. General ecological indices including Shannon-Weaver diversity, evenness, and Simpon's dominance index can be derived from the nematode community and provide

basic information about the richness, abundance, and diversity of the nematode community. However, they do not differentiate among nematode life strategies (Neher and Darby, 2009).

More information about soil health can be derived from the abundance or relative abundance (percent of total nematode population) of individual trophic groups based on their roles in the soil environment and ecosystem. Bacterivores feed on bacteria and may indicate an influx of nutrients or increased environmental stress depending on species (Ferris et al., 2001). Additionally, bacterivores can increase nutrient cycling in soil by mineralizing nutrients immobilized in bacteria, providing more nutrients for plants and other organisms (Woods et al., 1982; Anderson et al., 1983; Rosswall and Paustian, 1984; Ferris et al., 1998). Similarly, fungivores play a role in nutrient cycling (Anderson et al., 1983; Rosswall and Paustian, 1984; Chen and Ferris, 1999), although they are associated with a more stable, developed environment as fungi thrive in later stages of decomposition than bacteria (Ferris et al., 2001). Omnivores and predators often indicate a more structured soil food web with more fauna as they feed on lower trophic groups therefore relying on high populations of organisms at lower trophic levels to maintain their population (Ferris et al., 2001). A large abundance of beneficial (non-plant-parasitic) nematodes is associated with higher biological activity and resources in the soil.

Since plants are their food source, a large abundance of herbivores may indicate a diverse or productive plant community which is generally desired in an ecological setting (Bongers, 1990). Distinction is made between plant-parasitic nematodes, which are known to damage plants, and herbivores which include all nematodes that feed on plants regardless of whether they are capable of causing damage. Particularly in an agricultural setting, a soil with a large abundance of plant-parasitic nematodes is considered unhealthy because these nematodes reduce plant growth. However, since other herbivores (such as root-hair or algal feeders) have a negligible effect on plant growth (Yeates et al., 1993), they may indicate better soil and plant productivity and indicate some level of food web structure as plants are not present in very primitive systems.

Despite this, even within trophic groups different nematode taxa have very different life cycles and sensitivity to environmental stress, so it is difficult to make inferences about soil ecology based solely on trophic group abundances. To more

accurately and sensitively measure various aspects of soil health, a number of nematode community indices have been developed.

Table 1.1. Summary of nematode community indices.

Variable	Symbol	Calculation	Greater value Indicates
Shannon-Weaver Diversity Index		(genera relative abundance * ln(relative abundance)), summed for all genera	more diverse nematode community (more genera with more similar abundance)
Evenness		diversity divided by ln(# genera)	similar abundance among genera
Simpson's Dominance Index		relative abundance^2 summed for all genera	less diverse nematode community
Maturity Index	MI	average nematode c-p value excluding herbivores	less disturbed soil community
MI25	MI25	same as MI, but nemas with c-p of 1 excluded	less disturbance excluding enrichment
∑MI	∑MI	same as MI, but also includes herbivores	less disturbance, more established plant community
∑MI25	∑MI25	same as ∑MI, but nemas with c-p 1 excluded	less disturbance excluding enrichment; more established plant community
Plant Parasitic Index	PPI	average herbivore c-p value	more mature herbivore community; more plant production/diversity; less/more disturbed soil
Enrichment Index	EI	weighted‡, modified relative abundance of opportunistic nematodes	soil has more food and nutrient resources (enriched condition)
Basal Index	BI	weighted, modified relative abundance of stress-tolerant nemaotdes	more environmental stress, fewer resources (basal condition)
Structure Index	SI	weighted, modified relative abundance of high c-p nematodes	more trophic links (structured condition); later succession
Channel Index	CI	weighted ratio of fungivores to bacterivores	decomposition mediated by fungi more than bacteria (more advanced condition)
F/(F+B)	FFB	# fungivores/(# fungivores +bacterivores)	similar to CI
(F+B)/PP	FBPP	(# fungivores +bacterivores)/# herbivores	more favorable plant growth conditions

‡weights give more value to nematodes that are larger (consume more resources) or more strongly representative of the index (ex: more extreme enrichment opportunists have a larger weight in EI)

These indices are calculated based on both trophic group and life history strategy as measured by the colonizer-persister (*c-p*) value (1 to 5 scale) of each nematode in the community (Bongers, 1990). Nematodes with small *c-p* values (colonizers) are

similar to ecological “r-strategists” and have short life cycles, high reproductive rate, small size, and high tolerance to environmental stress. In contrast, nematodes with large *c-p* values (persisters) are similar to “k-strategists” and have long life cycles, low reproductive rates, large size, and low tolerance to environmental stress.

The maturity index (MI) measures disturbance of the soil system based on the average *c-p* value in the community, with higher values indicating less disturbance or later stages of succession (Bongers, 1990). Thus, a larger maturity index is generally associated with more mature, healthy soil. Bongers (1990) did not include plant-parasitic nematodes in the original maturity index because they are reflective of plant abundance and development, not solely soil condition. Instead, a plant parasite index (PPI) including only herbivores was created which may have a positive (Bongers et al., 1997; Bongers and Ferris, 1999) or negative (Neher and Campbell, 1996) relationship with disturbance. In contrast, Yeates (1994) proposed that plant community composition and production is part of soil community succession and health. Therefore, Yeates (1994) included all nematodes in an additional modified maturity index (ΣMI). Additional indices (ΣMI25, MI25) exclude opportunistic nematodes because these nematodes generally indicate recent enrichment. These indices examine soil disturbance ignoring recent enrichment effects (Bongers and Korthals, 1993; Yeates, 1994).

Maturity indices, as weighted averages, show if there are proportionally more persisters or more colonizers, but do not inform about the absolute abundance of either group. So, two soil communities could have the same maturity index value, but one soil could be much more biologically active with ten-fold more nematodes. To more sensitively detect soil processes and conditions, Ferris (2001) developed the following food web indices. The first three indices sensitively detect three common food web conditions: structured, enriched, and basal using weighted, modified relative abundances (percent of total nematode abundance) of nematode guilds (based on trophic group and *c-p* value) indicative of each condition. The structure index (SI) is a measure of the structure or number of links in the nematode trophic system with larger values indicating a more structured food web. Nematodes at higher trophic levels (omnivores and predators) and following persister life strategies are more common in structured systems. The enrichment index (EI) measures soil enrichment, defined as disturbance that causes an influx of nutrients or substrates including influxes due to organism death. Higher enrichment index values indicate more enrichment with the

characteristic group being very small *c-p* value (1 or 2) fungivores and bacterivores. The basal index (BI) indicates stressed, low resource conditions with higher basal index values indicating more basal conditions. Stress-tolerant fungivores and bacterivores (*c-p* value 2) that are present in almost any soil are the characteristic basal group (Ferris et al., 2001).

In addition to the three indices corresponding to food web conditions, Ferris (2001) developed the Channel Index (CI) to determine if decomposition pathways are primarily fungal or bacterial. The channel index is a modified ratio of the weighted abundance (more weight for greater *c-p* values) of fungivores to bacterivores. Larger channel index values indicate decomposition by fungi while smaller values indicate decomposition by bacteria (Ferris et al., 2001). A similar index takes the abundance of fungivores and divides it by fungivore plus bacterivore abundance (Neher and Campbell, 1996). This index, referred to as FFB, is more statistically robust than the fungivore to bacterivore ratio (FB) (Neher et al., 1995), but less refined than the channel index (Ferris et al., 2001). Whichever index is used, decomposition through fungal pathways is equated with a more soil system in later stages of ecological succession than decomposition through bacterial pathways (Neher et al., 1995; Neher and Campbell, 1996; Ferris et al., 2001). A final index takes the abundance of fungivores and bacterivores and divides it by herbivore abundance. Higher values of this index (FBPP) indicate a more healthy soil with values greater than one suggesting the benefits outweigh the drawbacks of the nematode community on plants (Wasilewska, 1989).

5. Influence of Crop Rotation on the Nematode Community

Soil ecology, particularly nematode community analysis is a narrow field, so there is limited research on how crop rotation impacts the nematode community. Therefore, rather than focusing on only corn-soybean rotations, a broad range of rotations are considered in the following review.

A long-term experiment near Winnepeg, Manitoba compared crop rotations: wheat-pea-wheat-flax, wheat-fababean green manure-wheat-flax, and spring wheat-alfalfa-alfalfa-flax after 13 years in rotation (Briar et al., 2012). Nematode community measures did not differ much between these systems, perhaps because they are all relatively long rotations including diverse crops. The only significant effect was a reduction in fungivores population and channel index value in the sequence including fababean green manure compared with the sequence with alfalfa.

A long-term experiment in Madagascar examined 25-27 years after establishment compared crop rotations (in no-till except where noted) including (1), corn-soybean with residue mulch, (2) common bean-soybean with *Pennisetum clandestinum* living mulch, (3) continuous corn with *Desmodium uncinatum* living mulch, (4) corn-soybean under conventional tillage, and (5) natural fallow (Djigal et al., 2012). The only meaningful differences were between continuous corn and the other treatments. Under continuous corn, plant-parasitic nematode populations were greater indicating increased disease pressure. Enrichment index values were increased, but maturity index and structure index values decreased under continuous corn indicating an enriched, but primitive nematode and soil community skewed toward enrichment-opportunist colonizers.

In a long-term experiment in Mexican subtropical highlands, wheat monoculture and wheat-corn annual rotation were compared in the 8-13th year of establishment (Govaerts et al., 2006). Cropping system did not affect the wheat parasitic *Pratylenchus thornei*, other plant-parasitic nematodes, or populations of non-plant-parasitic nematodes. Other indices were not calculated.

A long-term experiment in Australia compared wheat monoculture and wheat-lupin annual rotation both under additional residue management and tillage treatments in the 23rd year after establishment (Rahman et al., 2007). Overall free-living and plant-parasitic nematode populations were measured, but specific analyses were not conducted. Free-living nematodes were more populous with rotation than monoculture while plant-parasitic nematodes (*Pratylenchus* and *Paratylenchus*) favored monoculture. This suggests rotation resulted in a more balanced soil ecosystem.

In a study in Prince Edward Island, Canada, plant-parasitic and bacteria-feeding nematodes were assessed in potato, barley, and red clover phases of a three-year rotation where a single phase was planted each year (Carter et al., 2009). Host-specific plant-parasitic nematode populations increased in the phase containing the corresponding host crop. Bacterivore populations were increased under potato compared to barley or red clover.

A study in western Australia compared populations of nematode trophic groups between canola, wheat and lupin in the third year of a canola-wheat-lupin rotation where each phase was grown each year (Osler et al., 2000). In some seasons, total nematode, fungivore, and bacterivore populations were nearly twice as great in wheat than in other crops.

6. Summary

The relationship between the rotation yield effect in corn-soybean systems and agronomic or soil factors including soil nutrients, soil structure, soil moisture, plant root growth, and soil-borne disease have been extensively studied. From this research, it is clear that soil nutrients are not the only factor influencing the rotation effect. Plant-parasitc nematodes—particularly SCN—are likely to have a role in the rotation effect, but this role is not well-quantified. The relationships between non-pathogenic soil microbes and crop rotation are also poorly characterized. Current research suggests crop rotations influence the nematode community and soil ecology, but that impacts vary from system to system. Information on the influence of different corn-soybean rotations on the nematode community is very limited. The research described in the following chapters seeks to build on this knowledge of crop rotation, crop growth, plant-parasitic nematodes, and soil ecology.

Chapter 2: Interactions Between Corn-Soybean Crop Rotation, Crop Yield, and Plant-Parasitic Nematodes in a Long-Term Field Experiment

1. Introduction

Corn and soybean production are an integral part of agriculture in the United States and together represent a majority of agricultural production. In 2014, 37 and 34.3 million hectares of corn and soybean respectively were planted in the United States, 53.5% of total area planted to principal crops (NASS-USDA, 2014). Corn-soybean rotation has long been known to increase yield of both crops compared to monoculture, a phenomena known as the rotation effect, and the factors driving this are of interest. The most widely recognized benefit of corn-soybean rotation is maintance of soil nutrients, particularly nitrogen due to nitrogen-fixation by soybean (Peterson and Varvel, 1989; Meese et al., 1991; Omay et al., 1998). However, soil nutrients are not the only cause of the rotation effect as corn benefits from rotation with crops that do not fix nitrogen (Robinson, 1966; Barber, 1972; Bolton et al., 1976; Maloney et al., 1999), and soybean benefits from crop rotation despite fixing its own nitrogen (Crookston et al., 1991; Meese et al., 1991; Porter et al., 1997; Wilhelm and Wortmann, 2004; Salvagiotti et al., 2008). Additionally, a number of studies have established that the rotation effect occurs even when sufficient nutrients are supplied by fertilizer (Crookston et al., 1991; Meese et al., 1991; Porter et al., 1997; Howard et al., 1998; Wilhelm and Wortmann, 2004).

There is evidence that other agronomic factors including soil moisture (Copeland et al., 1993; Pedersen and Lauer, 2004), soil structure (Griffith et al., 1988; Nickel et al., 1995), and crop residue volume or chemical properties (Yakle and Cruse, 1984; Crookston et al., 1988; Crookston and Kurle, 1989; Nickel et al., 1995) may contribute to the rotation effect and that rotation influences crop physiology (Copeland and Crookston, 1992; Nickel et al., 1995; Pikul et al., 2012). Vesicular-arbuscular mycorrhizae (Johnson et al., 1991) and nutrient mineralization by microbes (Green and Blackmer, 1995; Gentry et al., 2001) may also contribute to the corn-soybean rotation effect. Additionally, corn-soybean rotation helps manage various pathogens and pests that reside or overwinter in plant residue and soil which can contribute to yield benefits of rotation (Gracia-Garza et al., 2002; Rousseau et al., 2007; Pedersen and Grau, 2010; Jirak-Peterson and Esker, 2011; Chu et al., 2013).

Another factor that may play an important role in the corn-soybean rotation effect is plant-parasitic nematodes. Soybean cyst nematode (SCN, *Heterodera glycines*) is the most damaging pathogen of soybean in the Midwestern United States (Koenning and Wrather, 2010) and there are many damaging plant-parasitic nematodes of corn as well (Norton and Hinz, 1976; Norton et al., 1978; Malek et al., 1980; Norton, 1984; Todd and Oakley, 1996). Soybean cyst nematode is host-specific to soybean and some other leguminous crops while most other field crops, including corn, are not hosts (Warnke et al., 2008). Consequently, rotation with corn is used to manage this nematode, so SCN is likely to play a role in the rotation effect in the Midwest (Noel and Edwards, 1996; Chen et al., 2001b; Porter et al., 2001; Conley et al., 2011). The interaction between crop rotation and plant-parasitic nematodes in corn production is not well-studied, so the role of these nematodes in declining corn yield under monoculture is not well-known.

A long-term research site in Waseca, Minnesota, involving various corn-soybean crop sequences provides a unique opportunity to investigate the role of plant-parasitic nematodes in the corn-soybean rotation effect. This site, along with identically designed partner sites, has been a platform for documenting the corn-soybean rotation effect even with sufficient soil nutrients (Crookston et al., 1991; Meese et al., 1991; Porter et al., 1997) as well as variable root density (Nickel et al., 1995), nutrient uptake by crops (Copeland and Crookston, 1992), soil moisture (Copeland et al., 1993), and vesicular arbuscular mycorhhizae populations (Johnson et al., 1991) under different crop sequences. In a previous study at the Waseca site, SCN population increased rapidly in the initial years soybean was grown and decreased rapidly when corn was grown, but SCN population was not significantly correlated with soybean yield (Porter et al., 2001). Trends in population of other plant-parasitic nematodes, including parasites of corn, have not been investigated at this site prior to the present study.

In the present study, nematicide was applied during to compare crop yield under various crop sequences with both normal and reduced nematode populations to demonstrate the impact of nematodes on crop yield particularly in interaction with crop rotation. Specifically, the objectives of this study were to: (i) determine the impact of corn-soybean crop sequences and nematicide application on plant-parasitic nematode populations; (ii) further document the impact of crop rotation on corn and soybean yield; and (iii) investigate the role of plant-parasitic nematodes in the rotation yield effect using nematicide.

Table 2.1. Corn (C) and soybean (S) cropping sequence treatments† in Waseca, MN.

	Crop sequence by year									
Treatments	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014
10-year rotation										
1.	C4	C5	S1	S2	S3	S4	S5	C1	C2	C3
2.	C3	C4	C5	S1	S2	S3	S4	S5	C1	C2
3.	C2	C3	C4	C5	S1	S2	S3	S4	S5	C1
4.	C1	C2	C3	C4	C5	S1	S2	S3	S4	S5
5.	S5	C1	C2	C3	C4	C5	S1	S2	S3	S4
6.	S4	S5	C1	C2	C3	C4	C5	S1	S2	S3
7.	S3	S4	S5	C1	C2	C3	C4	C5	S1	S2
8.	S2	S3	S4	S5	C1	C2	C3	C4	C5	S1
9.	S1	S2	S3	S4	S5	C1	C2	C3	C4	C5
10.	C5	S1	S2	S3	S4	S5	C1	C2	C3	C4
Annual rotation										
11.	Sc	Cs	Sc	Cs	Sc	Cs	Sc	Cs	Cs#	Sc#
12.	Cs	Sc	Cs	Sc	Cs	Sc	Cs	Sc	Sc#	Cs#
Continuous Monoculture										
13.	C	C	C	C	C	Cc	Cc	Cc	Cc	Cc
14.	Ss	Ss	Ss	Ss	Ss	Ss	Ss	Ss	Ss	Ss
Continuous; non-*Bt* corn & SCN-resistance soybean post-2010, alternating cultivars pre-1995										
15.	C	C	C	C	C	Cn	Cn	Cn	Cn	Cn
16.	Ss	Ss	Ss	Ss	Ss	Sr	Sr	Sr	Sr	Sr

† Cn and Cc are continuous corn recently (2010-2014) with non-*Bt* and *Bt* cultivars respectively; C is continuous corn; Cs# is 2nd (2013) or 1st (2014) yr corn previously in annual rotation; C1 through C5 are 1st to 5th yr corn after 5 yr of soybean; S1 through S5 are 1st to 5th yr soybean following 5 yr of corn; Sc# is 2nd (2013) or 1st (2014) yr soybean previously in annual rotation; Ss and Sr are continuous soybean recently with SCN-susceptible and resistant cultivars respectively. All soybeans, except Sr, were susceptible to SCN. From 2010-2014, all corn, except Cn, had *Bt* trait.

2. Materials and Methods

2.1 Experimental design

The study was conducted in Waseca, Minnesota at a field site where plots of various corn-soybean crop sequence treatments have been maintained continuously since 1982. The 16 crop sequences (Table 2.1) were: (i) 5 years corn followed by 5 years soybean with each phase grown each year such that both crops have treatments in years 1, 2, 3, 4, and 5 of monoculture every year; (ii) annual rotation with both crops planted each year; (iii) continuous monoculture of each crop; (iv) annual rotation between two cultivars--but crop monoculture--of each crop. Since 1995, sequence (iv) has been single-cultivar monoculture of each crop. Beginning in 2010, sequences (i), (ii), and (iii) were soybean susceptible to soybean cyst nematode (SCN, *Heterodera*

glycines) and *Bt* corn while sequence (iv) was SCN-resistant soybean cultivars with PI88788 resistance source and non-*Bt* corn cultivars. Before 2010, all sequences were SCN-susceptible soybean. From 2012-2013, sequence ii was not rotated, so crops were planted two years in a row rather than rotated annually. From 2010 onward, half of each plot was treated with in-furrow, granular nematicide to create a split-plot experiment arrangement with subplots 4.57 m wide by 7.62 m with 6 crop rows. In 2010 and 2011, terbufos nematicide (Counter 20G, AMVAC Chemical Corporation) was applied in-furrow at planting at 2.44 kg a.i./ha. In 2012-2014, aldicarb nematicide (Temik 15G, Bayer Crop Sciences) was applied in-furrow at planting at 2.94 kg a.i./ha. The crop sequence and nematicide experiment was a randomized complete block design with 4 replicates.

2.2 Site management

Corn and soybean were planted, with concurrent nematicide application to appropriate subplots, on May 20, 2010; June 2, 2011; June 1, 2012; June 3, 2013; and May 21, 2014. *Bt*-trait corn cultivar planted was De Kalb 46-61 in 2010-2012, and De Kalb 50-66 in 2013-2014. *Bt*-free corn hybrid planted was DeKalb 44-92 in 2010-2012, and DeKalb 50-67 in 2013-2014. SCN-susceptible soybean planted was Pioneer 91M90 in 2010-2011, and Pioneer 92Y22 from 2012-2014. SCN-resistant soybean planted was Pioneer 92Y90 in 2010-2011, and Pioneer 92Y12 in 2012-2014.

Plots were managed with conventional tillage with the site chisel plowed each fall and field cultivated each spring before planting. Glyphosate was applied as needed for post-emergence weed management at rates from 0.96 to 1.42 liters a.i./ha per application with single applications in 2011, 2013, 2014, and to 2012 corn; but 2 applications in 2010 and to 2012 soybeans. Insecticide was applied as needed with Lambda-cyhalthrin foliar insecticide applied on August 5, 2011 at 0.026 kg a.i./ha and August 19, 2014 at 0.028 kg/ha for soybean aphid (*Aphis glycines*) control.

Crops were fertilized such that soil nutrients should not have been a limiting factor. Nitrogen fertilizer was surface-broadcast without incorporation at 224 kg N/ha (2011-2014) or 191 kg N/ha (2010) in the form of urea with agrotain to corn plots after planting. Nitrogen fertilizer was applied on June 1, 2010; June 8, 2011; June 6, 2012; June 12, 2013; and June 11, 2014. In fall 2012 before plowing and spring 2014, after plowing, all plots received P in the form of triple super phosphate at 84 and 78 kg/ha respectively and K in the form of potash at 224 and 39 kg/ha respectively.

2.3 Soil sampling and nematode assessment

Soil samples for analysis of nematode populations were collected 2010-2014 at three time points during each season: spring (within 1 week prior to planting), midseason (45 to 64 days after planting), and fall (at harvest). Spring 2010 soil samples were taken from the main plots before nematicide application. All other soil samples for nematode analysis were taken from all subplots. From each subplot, 20 soil cores were taken in the two central rows (within 4 cm of plant rows) to a depth of 15 cm. Soil samples were homogenized by passing through a metal screen with 4 mm apertures before further processing. In 2010, soil samples were collected on May 19, July 6 (47 days after planting [DAP]), and October 18 (151 DAP). In 2011, soil samples were collected on May 16, July 18 (46 DAP), and October 20 (140 DAP). In 2012, soil samples were collected on May 30, July 24 (54 DAP), and October 8 (130 DAP). In 2013, soil samples were collected on June 3, August 6 (64 DAP), and October 8 (127 DAP). In 2014, soil samples were collected on May 19, July 7 (45 DAP), and October 9 (94 DAP).

Additional soil samples were taken from subplots that did not receive nematicide on July 11, 2013 (38 DAP) and June 25, 2014 (35 DAP) to analyze NO_3. From each subplot sampled, 10 cores were taken in the two central rows (within 4 cm of plant rows) to a depth of 15 cm.

Vermiform plant-parasitic nematode population density was determined for all soil samples collected in spring, midseason, and fall from 2010 to 2014. Vermiform nematodes from each subplot were extracted from a 100 cm^3 homogenized soil subsample using a modified sucrose floatation and centrifugation method (Jenkins, 1964). From this extraction, a subsample of nematodes from each subplot was identified morphologically to genus and soil population densities were calculated for vermiform stages of SCN, *Pratylenchus*, *Helicotylenchus*, and *Xiphinema*. These genera represent the four major plant-parasitic nematodes consistently present at the site. Vermiform stages of SCN included both males and juveniles.

Additionally, SCN egg population density was determined for all soil samples collected at spring, midseason, and fall except spring 2010. For SCN egg extraction, a 100 cm^3 soil subsample was taken from each homogenized subplot soil sample following storage at 4 °C. Soil was soaked in a 1.76% powder dishwasher detergent solution for at least 15 minutes, then SCN females and cysts were extracted from the soil using a

semiautomatic elutriator (Byrd et al., 1976), collected on nested 250-µm-aperture and 850-µm-aperture sieves, and centrifuged in 63% sucrose solution for 5 min at 1100 *g*. Cysts were emaciated with a mechanical crusher to release eggs (Faghihi and Ferris, 2000), which were collected in water and stored at 4 °C until population density was determined from counts of a subsample of eggs using a microscope.

Soil samples taken for NO_3 in 2013 and 2014 were air-dried and mechanically ground. A 100g subsample of this soil was assessed for NO_3 at the University of Minnesota Research Analytical Laboratory, St. Paul, MN. In 2013 and 2014, a 100g subsample of homogenized soil collected in spring from each plot that did not receive nematicide was air-dried and assessed for soil properties including organic matter (OM), pH, P (Bray P-1 extraction method), and K soil levels (University of Minnesota Research Analytical Laboratory, St. Paul, MN).

2.4. Crop yield measurement

Crop yields were determined based on the two central rows of each plot. Soybean yields were standardized to 13% moisture and corn yield was standardized to 15.5% moisture. Corn was harvested October 12, 2010; October 11, 2011; October 5, 2012; October 29, 2013; and October 21, 2014. Soybean was harvested October 5, 2010; October 4, 2011; October 2, 2012; October 10 2013; and October 8, 2014.

2.5. Statistical Analysis

Nematode data were analyzed separately for each season—except spring 2010--using two-way ANOVA with appropriate error terms for a split-plot arrangement. Vermiform nematode populations in spring 2010 and soil nutrient and property measurements were only determined for nematicide-free plots, so these were analyzed using one-way ANOVA within that season. Crop yields were analyzed separately for corn and soybean. Within each season, yield and nematode data were also combined across years and the combined data were analyzed using two-way, split-plot ANOVA. Spring data were combined from 2011-2014 while midseason and fall were combined from 2010-2014 because nematicide subplots were not sampled in spring 2010. Annual rotation treatments were removed from the combined data set because these treatments were disrupted in 2013 and 2014 and not the same across years (Table 2.1). ANOVA models were evaulated for homogeneity of variance using Levene's test and for normality of residuals graphically (Levene, 1960; Cook and Weisburg, 1999). When necessary, response variables were transformed to meet these assumptions. For

variables with significant crop sequence effects ($P \leq 0.05$), crop sequence treatment means were separated using Fischer's protected LSD ($P \leq 0.05$). All analyses were performed using R version 3.0 (The R Foundation for Statistical Computing, Vienna).

3. Results

In most seasons, for nematode and yield data combined across years, there were year by nematicide or year by crop sequence interactions (Table 2.2). Therefore, all results focus on analysis within individual seasons, not combined across years.

3.1 Soil Properties

In both 2013 and 2014; K, organic matter, and pH were not significantly affected by crop sequence, but both P and NO_3 were significantly affected by crop sequence (Table 2.3). In 2013, before planting P was greater under Ss and Sr than many other crop sequences and greater entering S3 than Cc. In 2014, P was greater under Ss and Sr than any other crop sequence. In 2013 and 2014, NO_3 was greater in corn than soybean sequences. In 2014, NO_3 was also greater in 1st-year corn than C2 and Cc.

3.2 Crop yield

From 2012-2014, when aldicarb nematicide was applied, the treatment with nematicide application significantly increased corn yields compared to the treatment without nematicide application (Table 2.4). Averaged across crop sequences, nematicide increased corn yield 3%, 9%, and 8% in 2012, 2013, and 2014 respectively. In 2010-2011, when terbufos was applied, nematicide did not affect corn yield.

In every year except 2013, crop sequence significantly affected corn yields (Table 2.4). When crop sequence effects on corn yields were significant, yields generally decreased significantly with increasing length of monoculture in the initial 3 years of monoculture. In most years, corn yields were not significantly different among sequences in 3 or more years of monoculture. First-year corn yield was significantly greater following 5 years than 1 year of soybean in 2010, but similar between the two sequences in other years. Corn yield was significantly greater under Cc (Bt corn) than Cn (Non-Bt corn) in 2014, but similar in all other years.

In 2012, there was also significant crop sequence by nematicide interaction for corn yields (Table 2.4) with significant crop sequence effects for the treatment with nematicide and the treatment without nematicide (Table 2.5). In both cases, corn yields decreased with increasing length of monoculture as significant differences were primarily between sequences separated by 2 or more years in monoculture.

Table 2.2. Plant-parasitic nematode populations and crop yields as influenced by crop sequences and nematicide application for 2010-2014 combined.

	Helicotylenchus						*Pratylenchus*					
	Pi†	‡	Pm		Pf		Pi		Pm		Pf	
ANOVA (*F* values)												
Rotation (R)	17.47	**	18.41	**	12.91	**	69.51	**	73.13	**	54.60	**
Year (Y) x R	1.88	**	1.71	**	0.98		1.95	**	1.93	**	1.23	
Nematicide (N)	8.35	**	63.34	**	251.4	**	2.29		72.98	**	127.7	**
N x Y	6.10	**	11.79	**	29.39	**	2.77	*	8.92	**	20.79	**
R x N	1.61		2.63	**	1.51		1.07		1.45		2.56	**
Y x R x N	0.79		0.89		1.10		0.73		1.13		0.99	
	vermiform SCN						SCN eggs					
	Pi†		Pm		Pf		Pi		Pm		Pf	
ANOVA (*F* values)												
Rotation (R)	78.09	**	82.87	**	88.48	**	67.32	**	68.66	*	72.19	*
Year (Y) x R	2.64	**	3.31	**	1.92	**	1.62	*	3.06	*	2.11	*
Nematicide (N)	7.11	**	1.10		3.08		5.75	*	3.43		10.90	*
N x Y	2.49		0.94		3.71	**	0.56		1.48		2.35	
R x N	1.56		0.74		2.34	**	1.07		1.01		1.86	*
Y x R x N	1.49	*	1.55	*	0.99		0.80		1.14		0.89	
	Xiphinema						Corn yield				Soybean yield	
	Pi†		Pm		Pf							
ANOVA (*F* values)												
Rotation (R)	1.35		1.55		4.75	**	41.48	**			18.62	**
Year (Y) x R	0.86		1.28		1.22		1.58				0.91	
Nematicide (N)	0.02		12.13	**	45.25	**	12.87	**			25.00	**
N x Y	0.78		5.78	**	17.56	**	7.50	**			12.59	**
R x N	0.84		1.89	*	1.57		1.69				0.67	
Y x R x N	1.20		1.31		0.72		1.24				1.28	

† Pi, Pm, Pf are mean population densities prior to planting, at midseason, and at harvest respectively.

* and ** represent significant effects at $P \leq 0.05$ *and* $P \leq 0.01$ respectively.

Table 2.3. Soil nutrients and properties as influenced by crop sequences and nematicide application in 2013-2014.

	2013							2014						
	P†		K	NO3		%OM	pH	P		K	NO3		%OM	pH
	----------mg/kg----------							----------mg/kg----------						
Rotation•														
Cn	16	cd	161	56	a	5.8	6.2	11	b	143	41	ab	5.6	6.3
Cc	13	d	148	55	a	5.8	6.2	12	b	143	39	b	5.3	6.5
Cs#	20	cd	155	65	a	5.6	6.5	17	b	131	51	a	5.8	6.6
C1	19	cd	145	69	a	5.1	6.7	19	b	148	52	a	5.5	6.8
C2	22	bcd	143	59	a	5.4	6.6	15	b	137	39	b	5.2	6.5
C3	15	cd	151	67	a	5.3	6.7	18	b	146	43	ab	5.6	6.8
C4	24	bcd	160	59	a	5.6	6.4	13	b	155	45	ab	5.4	6.3
C5	18	cd	155	57	a	5.6	6.9	17	b	152	49	ab	5.9	6.2
S1	22	bcd	163	3	b	5.3	6.4	12	b	139	3	c	5.9	6.1
S2	20	cd	163	5	b	5.6	6.5	16	b	140	4	c	5.7	6.4
S3	26	abc	163	4	b	5.5	6.4	14	b	145	4	c	5.6	6.4
S4	20	cd	154	5	b	5.1	6.7	17	b	147	3	c	5.6	6.3
S5	20	cd	150	5	b	5.5	6.9	15	b	140	3	c	5.1	6.6
Sc#	23	bcd	154	4	b	5.8	6.6	13	b	143	2	c	5.7	6.3
Ss	34	ab	147	6	b	5.2	6.9	29	a	135	3	c	5.3	6.7
Sr	38	a	137	4	b	5.4	6.8	34	a	136	3	c	5.3	6.9
ANOVA (*F* values)														
Rotation (R)	2.00	*	0.47	31.5	**	0.94	1.50	3.72	**	0.33	67.5	**	0.85	1.54

† P,K,OM (organic matter), and pH were measured before planting while NO3 was measured at 38 (2013) and 35 (2014) days after planting.
‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor (nematicide or rotation).
• Cn and Cc are continuous corn recently (2010-2014) with non-*Bt* and *Bt* cultivars respectively ; Cs# is 2nd (2013) or 1st (2014) yr corn previously in annual rotation; C1 through C5 are 1st to 5th yr corn after 5 yr of soybean; S1 through S5 are 1st to 5th yr soybean following 5 yr of corn; Sc# is 2nd (2013) or 1st (2014) yr soybean previously in annual rotation; Ss and Sr are continuous soybean recently (2010-2014) with SCN-susceptible and resistant cultivars respectively. All soybeans, except Sr, were SCN-susceptible.

* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively.

Table 2.4. Corn yields (Mg/ha) as influenced by crop sequences and nematicide in 2010-2014.

	2010†		2011		2012		2013		2014	
Rotation										
Cn	11.4	de	9.7	d	11.5	cd	12.1		7.6	d
Cc	11.2	e	9.7	d	10.6	d	12.0		8.9	c
Cs#	13.6	b	11.3	ab	13.5	ab	12.6		12.3	a
C1	15.5	a	12.0	a	14.0	a	14.2		12.4	a
C2	12.5	c	11.1	abc	12.8	abc	13.1		10.6	b
C3	11.5	de	10.5	bcd	11.5	cd	12.5		9.2	c
C4	11.3	de	10.3	cd	12.1	bcd	12.0		9.2	c
C5	12.1	cd	9.9	d	11.4	cd	11.9		9.1	c
Nematicide										
Not applied	12.4		10.8		12.1	B	12.0	B	9.4	B
Applied	12.6		10.4		12.4	A	13.1	A	10.2	A
ANOVA (*F* values)										
Rotation (R)	26.44	**	7.08	**	5.13	**	2.39		21.25	**
Nematicide (N)	0.08		1.52		5.69	*	30.79	**	17.30	**
R x N	1.06		0.71		4.93	**	1.09		1.11	

‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor (nematicide or rotation).

• Cn and Cc are continuous corn recently (2010-2014) with non-*Bt* and *Bt* cultivars respectively; Cs# is corn in annual rotation 2010-2012, 2nd yr corn previously in annual rotation in 2013, and 1st yr corn following 2nd yr soybean previously in annual rotation in 2014; C1 through C5 are 1st to 5th yr corn after 5 yr of soybean.

* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively.

Nematicide applications significantly increased soybean yields compared to the treatment without nematicide application in 2012 and 2013—2 of the 3 years when aldicarb was applied (Table 2.6). Averaged across crop sequences, nematicide increased soybean yields 7% and 11% in 2012 and 2013. Crop sequence significantly affected soybean yields every year except 2012 (Table 2.6). Soybean yields generally declined with increasing years in soybean, but rates of decline were small as only sequences separated by two or more years in monoculture were significantly different. In 2013, soybean yield was significantly greater in SCN-resistant than SCN-susceptible long-term soybean monoculture, but yields were similar between the two sequences in other years. Soybean yields were similar in annual rotation (2nd-year corn previously in annual rotation in 2013) and 10-year rotation when comparing similar lengths in monoculture (2 years in 2013, 1 year otherwise), except 2011 when 1st-year soybean yield following 5 years corn was greater than soybean in annual rotation.

Table 2.5. Corn yields (Mg/ha) and relative corn yields (% of maximum yielding crop sequence) as influenced by crop sequences with or without nematicide application in 2012.

	Yield				Relative Yield	
	Nematicide		No nematicide		Nematicide	No nematicide
Rotation •	----------yield (Mg/ha)----------					
Cn	10.8	d	12.2	ab	75%	89%
Cc	11.0	d	10.2	c	77%	75%
Cs	13.7	ab	13.4	a	95%	98%
C1	14.4	a	13.7	a	100%	100%
C2	12.8	abc	12.8	a	89%	93%
C3	12.2	bcd	10.8	bc	85%	79%
C4	11.8	cd	12.4	ab	82%	91%
C5	12.3	bcd	10.5	c	86%	77%
ANOVA (*F* values)						
Rotation (R)	4.58	**	5.45	**		

‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor (nematicide or rotation).

• Cn and Cc are continuous corn recently (2010-2014) with non-*Bt* and *Bt* cultivars respectively; Cs# is corn in annual rotation 2010-2012, 2nd yr corn previously in annual rotation in 2013, and 1st yr corn following 2nd yr soybean previously in annual rotation in 2014; C1 to C5 are 1st to 5th yr corn after 5 yr soybean.

* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively.

Table 2.6. Soybean yields as influenced by crop sequences and nematicide in 2010-2014.

	2010†		2011		2012		2013		2014	
Rotation•										
S1	3.44	ab	3.49	a	2.80		3.35	a	2.06	a
S2	3.47	a	3.33	ab	2.67		3.25	ab	1.80	ab
S3	3.20	abc	3.10	cd	2.60		3.14	ab	1.75	ab
S4	3.43	ab	2.98	d	2.40		3.08	ab	1.63	b
S5	3.23	abc	3.06	cd	2.44		2.94	b	1.70	b
Sc#	3.16	bc	3.23	bc	2.60		3.06	ab	1.78	ab
Ss	2.95	c	2.72	e	2.29		2.53	c	1.23	c
Sr	3.02	c	2.66	e	2.58		3.02	ab	1.48	bc
Nematicide										
Not applied	3.26		3.08		2.46	B	2.91	B	1.68	
Applied	3.23		3.10		2.64	A	3.24	A	1.68	
ANOVA (*F* values)										
Rotation (R)	3.54	*	12.62	**	1.20		3.88	**	4.48	**
Nematicide (N)	1.38		0.15		14.75	**	59.90	**	0.07	
R x N	2.06		0.61		0.69		1.84		1.17	

† Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor (nematicide or rotation).

• S1 through S5 are 1st to 5th yr soybean following 5 yr of corn; Sc# is soybean in annual rotation 2010-2012, 2nd yr soybean previously in annual rotation in 2013, and 1st yr soybean following 2nd yr corn previously in annual rotation in 2014; Ss and Sr are continuous soybean recently (2010-2014) with SCN-susceptible and resistant cultivars respectively. All soybeans, except Sr, were SCN-susceptible.

* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively.

3.3 Soybean cyst nematode eggs

Nematicide applications significantly decreased SCN egg populations in midseason 2011, fall 2012, and fall 2013 (Tables 2.7 and 2.8) with population reductions of 47%, 71%, and 49%, respectively compared to treatment without nematicide application. Crop sequence significantly affected SCN egg populations every season in which samples were taken (Tables 2.7 and 2.8). SCN egg populations generally increased in soybean and decreased in corn—particularly in the first three years of monoculture—so populations were significantly greater in soybean than corn monoculture for most sequences (Tables 2.7 and 2.8). In the initial years of soybean monoculture, SCN egg populations generally increased as years in SCN-susceptible soybean increased although the details of this trend varied by season. In most seasons, SCN populations also reached statistical maximums where further increases in the number of years in soybean did not significantly increase SCN populations.

The details of these trends varied by season, as SCN populations reached a maximum after 2 (fall 2010), 3 (midseason 2010, midseason & fall 2011, spring 2012, fall 2014), 4 (midseason 2012, fall 2012, spring 2013, & midseason 2013), or 5 years of soybean monoculture. In fall 2012, SCN egg density was smaller under Ss than S4 suggesting a decline in long-term soybean monoculture. SCN egg population was moderate at the site with SCN populations generally under 5,000 eggs/100 cm^3 soil even in soybean monoculture (Tables 2.7 and 2.8). SCN egg populations were greater in SCN-susceptible than SCN-resistant long-term soybean monoculture in all seasons except midseason 2010 and 2011.

SCN egg populations generally decreased significantly in the initial years in corn monoculture although the details of this trend varied by season (Tables 2.7 and 2.8). In most seasons, SCN eggs reached small densities—always below 100 eggs/100 cm^3 soil—at a certain number of years in corn beyond which further increases in years in corn did not significantly change SCN egg populations. The length of corn monoculture needed to reach minimum populations for particular seasons varied with minimums reached after 1 (fall 2012), 3 (2010 midseason 2014, and fall 2014), 4 (midseason and fall 2011, and spring 2014) or 5 (spring 2013) years of corn monoculture. In other seasons (spring 2012, midseason 2012, and midseason 2013), SCN only reached minimum populations in long-term corn monoculture (Cc or Cn). In comparing annual and 10-year rotations, SCN egg populations in similar lengths of monoculture (2 years in midseason 2013 to spring 2014, 1 year otherwise) were significantly greater following 1 than 5 years of corn, but similar following 1 or 5 years of soybean in most seasons.

There were significant crop sequence by nematicide interactions in spring 2011 and fall 2013 (Tables 2.7 and 2.8). In spring 2011, there were significant crop sequence effects with nematicide treatment and no-nematicide treatment (Table 2.9), and trends were similar for both treatments with population densities increasing with soybean monoculture and decreasing with corn monoculture. However, population density increase in soybean monoculture was more rapid with nematicide than without nematicide. In fall 2013, there were significant crop sequence effects without nematicide, but there were no significant crop sequence effects with nematicide application (Table 2.9).

Table 2.7. Soybean cyst nematode egg population densities as influenced by crop sequences and nematicide application in 2010-2012.

	2010				2011						2012					
	Pm†	‡	Pf		Pi		Pm		Pf		Pi		Pm		Pf	
Rotation•																
Cn	11	d	19	fg	13	f	28	de	6	g	6	i	24	g	22	f
Cc	25	d	14	fg	13	f	8	e	44	fg	41	hi	19	g	49	f
Cs	2442	ab	1402	de	1868	bcd	660	ab	450	de	211	bcd	1097	abc	866	ef
C1	2414	a	1705	bcd	2421	abc	985	ab	967	d	1452	abc	1324	a	744	ef
C2	1408	bc	749	e	1244	cd	619	abc	595	de	669	cd	344	defg	227	f
C3	74	d	28	fg	1153	de	1032	abc	634	de	236	def	196	defg	85	f
C4	119	d	41	fg	88	f	23	de	13	fg	382	fg	567	def	582	ef
C5	96	d	3	g	125	f	39	de	39	fg	28	ghi	36	fg	55	f
S1	44	d	267	f	88	f	49	de	506	ef	35	gh	86	efg	517	ef
S2	1321	c	1820	abcd	806	ef	316	cde	1972	cd	285	efg	135	efg	2532	de
S3	3211	a	3172	a	1355	cd	732	ab	5369	a	850	de	843	bcd	5285	cd
S4	2382	a	2833	ab	2571	abc	1136	a	4838	a	2339	ab	1466	ab	12138	a
S5	2269	ab	2406	abc	3316	a	696	ab	4714	a	3624	a	1785	a	8780	ab
Sc	925	c	1530	cd	886	de	677	abc	2381	bc	1322	def	353	cde	5877	bc
Ss	3208	a	2791	abc	3130	ab	1060	ab	3194	ab	2679	ab	1774	a	7742	bc
Sr	2447	a	504	e	867	de	313	bcd	183	ef	127	efg	38	fg	149	f
Nematicide																
Not applied	1477		1311		1387		684	A	1675		964		704		4415	A
Applied	1322		1122		1118		365	B	1662		822		556		1291	B
ANOVA (*F* values)																
Rotation (R)	22.72	**	26.48	**	13.01	**	5.58	**	26.77	**	14.59	**	9.58	**	11.34	**
Nematicide (N)	0.91		1.48		2.82		15.8	**	0.16		0.01		0.43		13.98	**
R x N	0.86		0.94		2.14	*	0.96		0.45		0.57		0.59		1.46	

† Pi, Pm, Pf are mean eggs/100 cm^3 soil prior to planting; 47 (2010), 46 (2011), or 54 (2012) days after planting; and at harvest respectively.
‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor.
• Cn and Cc are continuous corn with non-*Bt* and *Bt* cultivars respectively since 2010; Cs is corn in annual rotation; C1, C2, C3, C4, and C5 are 1st, 2nd, 3rd, 4th, and 5th yr corn following 5 yr of soybean; S1, S2, S3, S4, and S5 are 1st, 2nd, 3rd, 4th, and 5th yr soybean following 5 yr of corn; Sc is soybean in annual rotation; Ss is continuous SCN-susceptible soybean; and Sr is continuous soybean (SCN-resistant cultivar since 2010). All soybeans, except Sr, were SCN-susceptible.
* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively.

Table 2.8. Soybean cyst nematode egg population densities as influenced by crop sequences and nematicide application in 2013-2014.

	2013						2014					
	Pi†	‡	Pm		Pf		Pi		Pm		Pf	
Rotation•												
Cn	100	ef	3	g	50	c	44	e	37	d	13	f
Cc	91	f	13	fg	29	bc	22	e	88	d	42	ef
Cs#	669	def	428	bcd	186	b	206	ab	1242	ab	595	cde
C1	6404	a	3213	a	1986	a	4306	a	2477	a	2100	ab
C2	811	de	236	d	153	b	2550	ab	2447	ab	1388	abc
C3	258	ef	136	de	38	bc	225	d	113	d	117	ef
C4	327	def	69	ef	100	b	72	e	118	d	91	ef
C5	432	ef	147	fg	258	bc	303	cd	92	d	79	ef
S1	35	f	55	fg	224	bc	338	e	132	d	466	def
S2	158	ef	455	cd	1117	a	156	de	78	d	184	ef
S3	1724	cd	1216	abc	2579	a	900	bcd	477	bc	1746	ab
S4	3739	bc	2166	ab	2955	a	1353	abc	931	ab	1891	ab
S5	7520	a	4119	a	4397	a	3056	ab	1578	ab	2291	a
Sc#	3013	bc	1861	a	2539	a	1922	de	160	cd	1119	bcd
Ss	5350	ab	2985	a	4338	a	3956	a	2205	a	2389	a
Sr	140	ef	186	de	223	b	150	de	79	d	131	ef
Nematicide												
Not applied	1988		1236		1795	A	1279		981		1149	
Applied	1772		919		909	B	1160		680		897	
ANOVA (*F* values)												
Rotation (R)	16.35	**	1.97	*	10.78	**	8.62	**	11.26	**	10.12	**
Nematicide (N)	0.77		1.37		7.69	**	0.07		2.45		3.63	
R x N	1.06		0.74		1.99	*	0.77		0.86		1.10	

† Pi, Pm, Pf are mean eggs/100 cm^3 soil prior to planting, 64 (2013) or 47 (2014) days after planting, and at harvest respectively.

‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor.

• Cn and Cc are continuous corn recently (2010-2014) with non-*Bt* and *Bt* cultivars respectively; Cs# is 2nd (2013) or 1st (2014) yr corn previously in annual rotation; C1 through C5 are 1st to 5th yr corn after 5 yr of soybean; S1 through S5 are 1st to 5th yr soybean following 5 yr of corn; Sc# is 2nd (2013) or 1st (2014) yr soybean previously in annual rotation; Ss and Sr are continuous soybean recently with SCN-susceptible and resistant cultivars respectively.

* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively.

Table 2.9. SCN population densities as influenced by crop sequences with or without nematicide application.

	SCN eggs							
	2011 Pi†				2013 Pf			
	Nematicide		No nematicide		Nematicide		No nematicide	
Rotation•								
Cn	10	h	16	e	91		10	e
Cc	13	h	13	e	38		21	de
Cs#	2810	ab	925	de	163		210	de
C1	2469	abc	2372	bcd	1388		2584	bcd
C2	1538	bcd	950	de	53		253	de
C3	679	efg	1628	cde	19		57	de
C4	110	gh	66	e	188		13	e
C5	166	fgh	85	e	94		422	de
S1	72	gh	103	e	88		360	de
S2	169	fgh	1444	cde	997		1238	cde
S3	1022	de	1688	cde	2904		2254	cde
S4	1469	cde	3672	ab	807		5103	ab
S5	2466	abc	4166	a	3235		5560	a
Sc#	707	de	1066	cde	2032		3047	bc
Ss	3472	a	2788	abc	2094		6582	a
Sr	588	def	1146	cde	34		413	de
ANOVA (F values)								
Rotation (R)	11.66	**	4.51	**	1.65		7.21	**
	vermiform SCN							
	2012 Pi				2013 Pf			
	Nematicide		No nematicide		Nematicide		No nematicide	
Rotation•								
Cn	1	f	2	f	0		0	c
Cc	2	ef	4	ef	0		0	c
Cs#	49	ab	41	abc	36		10	b
C1	57	ab	64	ab	93		176	a
C2	58	ab	20	cd	37		8	b
C3	36	abc	26	bcd	23		10	b
C4	17	cd	11	de	4		0	c
C5	1	f	1	f	0		12	b
S1	1	f	7	de	6		0	c
S2	9	cd	20	de	42		76	a
S3	30	bcd	10	de	47		187	a
S4	54	ab	74	a	83		160	a
S5	102	a	64	ab	76		190	a
Sc#	17	cd	16	cd	77		138	a
Ss	44	ab	101	a	85		229	a
Sr	8	de	4	ef	0		4	bc
ANOVA (F values)								
Rotation (R)	8.71	**	10.38	**	10.88		24.06	**

† Pi and Pf are mean nematodes or eggs per 100 cm3 soil prior to planting; and at harvest respectively.
‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$).
• Cn and Cc are continuous corn with non-*Bt* and *Bt* cultivars respectively since 2010; Cs#, corn in annual rotation except 2013 which is 2nd yr corn previously in annual rotation; C1, C2, C3, C4, and C5 are 1st, 2nd, 3rd, 4th, and 5th yr corn following 5 yr of soybean; S1, S2, S3, S4, and S5 are 1st, 2nd, 3rd, 4th, and 5th yr soybean following 5 yr of corn; Sc#, soybean in annual rotation except 2013 which is 2nd yr soybean previously in annual rotation; Ss and Sr are continuous soybean with susceptible and resistant cultivars.
* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively.

3.4 Vermiform soybean cyst nematode

Nematicide applications significantly decreased vermiform SCN populations, which included both males and juveniles, in fall 2012, spring 2013, and midseason 2014 (Tables 2.10 and 2.11) with population reductions of 72%, 26%, and 24% respectively compared to without nematicide application. There were significant crop sequence effects in every season nematodes were sampled (Tables 2.10 and 2.11). Vermiform SCN vermiform populations increased in SCN-susceptible soybean monoculture and decreased in corn monoculture—particularly in the first three years of monoculture. This lead to significantly greater vermiform SCN populations in soybean than corn monoculture for many sequences. In many seasons, vermiform SCN populations also reached apparent maximum and minimum populations densities at a certain number of years in soybean and corn respectively with further increases in length of monoculture not significantly changing population densities (Tables 2.10 and 2.11).

In some seasons, vermiform SCN population reached maximum populations following 3 (midseason & fall 2010, spring 2011, fall 2011, and fall 2014), 4 (midseason 2011, midseason 2012, fall 2012, and spring 2013), or 5 (midseason 2013, spring 2014) years of SCN-susceptible soybean monoculture. In some seasons, vermiform SCN population densities were greatest in long-term monoculture (midseason 2011, fall 2013, sping and midseason 2014) suggesting population densities increased for more than 5 years. In a few seasons the population densities in long-term SCN-susceptible soybean monoculture (Ss) were significantly smaller than the greatest population densities in sequences in 10-year rotation (S3 in fall 2010, S5 in fall 2011 and spring 2013). Vermiform SCN populations were significantly greater in SCN-susceptible than SCN-resistant long-term soybean monoculture except in 2010.

In corn monoculture, vermiform SCN populations reached minimum populations-always near minimum detectable levels-- following 1 (midseason & fall 2010), 2 (spring 2010), 3 (spring 2011, midseason & fall 2014), 4 (midseason and fall 2011, midsean and fall 2013), or 5 (midseason and fall 2012) years of corn monoculture. In some seasons (midseason 2012, spring 2013, and spring 2014), vermiform SCN populations were smallest in long-term corn monoculture (Cc), although populations were similar among most sequences in more than 3 years of corn monoculture (Tables 2.10 and 2.11).

In some seasons, SCN populations differed between annual and 10-year rotation. In most seasons from 2010 to spring 2013, population densities before planting

or in 1st-year of soybean were greater following 1 than 5 years of corn respectively. Before planting, vermiform SCN populations were greater entering C1 than Cs–following 1 and 5 years of soybean respectively–in 2011 and 2014. However, in midseason and fall, vermiform SCN populations in these sequences were similar.

There were significant nematicide by crop sequence interactions in spring 2012 and fall 2013 (Table 2.10). In spring 2012, there were significant crop sequence effects on vermiform SCN populations in nematicide as well as no-nematicide treatments and trends in populations across sequences were similar under the two nematicide treatments (Table 2.9). Vermiform SCN population densities increased in soybean monoculture and reached maximum populations following 4 years in soybean. Population densities decreased in corn monoculture and reached minimum populations following 4 years in corn. In fall 2013, crop sequence affected vermiform SCN populations only without nematicide application (Table 2.9). Without nematicide application, vermiform SCN populations were greater under soybean than corn sequences, excluding 1-year sequences.

3.5 *Pratylenchus*

Nematicide applications significantly reduced *Pratylenchus* soil populations every season following spring 2012--when aldicarb was first applied—compared to the treatment without nematicide application (Tables 2.12 and 2.13). Averaged across crop sequences, aldicarb nematicide reduced *Pratylenchus* soil populations 76%, 77%, and 64% in midseason 2012-2014; 90%, 87%, and 75% in fall 2012-2014; and 31% and 56% in spring 2013 and 2014 compared to non-nematicide treatment.

Crop sequence significantly affected *Pratylenchus* populations every season of the study (Tables 2.12 and 2.13). *Pratylenchus* populations decreased in soybean monoculture and increased in corn monoculture—particularly in the first 3 years of monoculture—leading to significantly greater *Pratylenchus* populations under corn than soybean monoculture for many sequences (Tables 2.12 and 2.13). In corn, *Pratylenchus* reached population maximums at a particular number of years in corn—which varied by season--and further increases in years in corn did not significantly change population densities. Specifically, maximum populations were reached following 3 (midseason and fall 2010, midseason and fall 2011), 4 (fall 2014), or 5 (spring 2010, spring 2011, spring 2014, and midseason 2014) years in corn monoculture.

Table 2.10. Vermiform *Heterodera* population densities as influenced by crop sequences and nematicide application in 2010-2012.

	2010						2011						2012					
	Pi†	‡	Pm		Pf		Pi		Pm		Pf		Pi		Pm		Pf	
Rotation•																		
Cn	0	f	0	c	5	d	6	e	10	ef	3	h	1	h	9	ef	0	g
Cc	5	ef	1	c	8	d	1	e	2	f	3	h	3	gh	2	ef	0	g
Cs	223	ab	123	bc	143	abc	98	bc	51	d	27	efg	16	ab	33	bcd	18	de
C1	250	ab	146	bc	116	abcd	193	a	62	cd	57	cd	60	ab	30	bc	14	de
C2	88	d	49	c	58	bcd	84	c	63	cd	36	de	39	abc	9	def	6	f
C3	20	e	5	c	24	cd	59	cd	38	d	29	def	31	bcd	11	cde	6	f
C4	23	e	9	c	40	bcd	6	e	3	ef	3	h	14	def	13	def	14	f
C5	5	ef	10	c	0	d	3	e	5	ef	3	h	1	h	2	f	0	g
S1	8	ef	15	c	25	cd	3	e	14	ef	20	fgh	4	fgh	5	ef	6	ef
S2	100	cd	111	bc	123	bcd	40	de	18	e	52	de	15	de	20	ef	33	cd
S3	193	abc	286	abc	213	a	80	c	91	bc	158	ab	20	cde	71	b	105	bc
S4	228	ab	293	ab	159	abcd	193	a	168	a	159	ab	64	ab	174	a	193	ab
S5	275	a	223	bc	154	ab	201	a	121	ab	178	a	83	a	222	a	218	a
Sc	83	d	131	bc	103	bcd	73	c	72	cd	134	ab	45	cde	59	b	167	ab
Ss	238	ab	335	a	114	bcd	175	ab	122	ab	111	bc	73	a	195	a	187	ab
Sr	165	bcd	159	bc	32	cd	40	cd	40	d	6	gh	6	efg	7	def	8	fg
Nematicide																		
Not applied			107		88		79		54		61		30		56		95	A
Applied			130		78		79		54		65		29		52		26	B
ANOVA (*F* values)																		
Rotation (R)	20.1	**	1.93	*	2.14	*	17.8	**	18.2	**	21.4	**	13.2	**	16.0	**	26.6	**
Nematicide (N)			0.89		0.96		0.46		0.05		0.35		0.00		1.53		14.2	**
R x N			0.85		0.84		1.64		0.98		0.58		1.98	*	0.87		0.95	

† Pi, Pm, Pf are mean population densities (nemas/100 cm^3 soil) prior to planting; 47 (2010), 46 (2011), or 54 (2012) days after planting; and at harvest.
‡ Different letters in the same column indicate significant differences (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor.
• Cn and Cc are continuous corn with non-*Bt* and *Bt* cultivars respectively since 2010; Cs is corn in annual rotation; C1, C2, C3, C4, and C5 are 1st, 2nd, 3rd, 4th, and 5th yr corn following 5 yr of soybean; S1, S2, S3, S4, and S5 are 1st, 2nd, 3rd, 4th, and 5th yr soybean following 5 yr of corn; Sc is soybean in annual rotation; Ss is continuous SCN-susceptible soybean; and Sr is continuous soybean (SCN-resistant cultivar since 2010). All soybeans, except Sr, were SCN-susceptible.
* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively.

Table 2.11. Vermiform *Heterodera* population densities as influenced by crop sequences and nematicide application in 2013-2014.

	2013						2014					
	Pi†	‡	Pm		Pf		Pi		Pm		Pf	
Rotation•												
Cn	7	gh	22	e	0	e	2	f	2	d	0	g
Cc	3	h	23	e	0	e	3	f	1	d	0	g
Cs#	28	efg	19	cd	23	cd	6	ab	89	bc	51	bcd
C1	358	a	100	a	135	a	211	a	147	ab	89	abc
C2	50	ef	13	d	22	d	53	ab	59	c	60	bcd
C3	25	fg	3	d	16	d	15	cd	7	d	11	fg
C4	20	fg	4	e	2	e	4	f	6	d	3	g
C5	14	gh	38	e	6	e	11	de	13	d	15	efg
S1	6	gh	7	e	3	e	9	ef	25	d	44	def
S2	12	gh	12	bc	59	bc	10	ef	9	d	40	cde
S3	98	de	66	ab	117	ab	74	bc	65	c	107	ab
S4	236	bc	105	ab	121	ab	98	ab	114	bc	124	a
S5	398	a	114	ab	133	ab	138	ab	128	b	137	a
Sc#	134	cd	68	ab	107	ab	113	ef	14	d	56	def
Ss	240	b	104	a	157	a	153	a	221	a	107	ab
Sr	12	gh	10	e	2	e	6	ef	7	d	6	g
Nematicide												
Not applied	115	A	46		76		51		50	b	63	
Applied	85	B	42		38		63		66	a	52	
ANOVA (*F* values)												
Rotation (R)	26.41	**	6.42	**	27.67	**	16.35	**	15.55	**	12.66	**
Nematicide (N)	5.56	*	0.30		3.48		0.33		4.04	*	0.35	
R x N	1.51		1.10		2.90	**	1.03		1.26		1.15	

† Pi, Pm, Pf are mean nematodes/100 cm^3 soil prior to planting, 64 (2013) or 47 (2014) days after planting, and at harvest respectively.

‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor.

• Cn and Cc are continuous corn recently with non-*Bt* and *Bt* cultivars respectively ; Cs# is 2nd (2013) or 1st (2014) yr corn previously in annual rotation; C1 through C5 are 1st to 5th yr corn after 5 yr of soybean; S1 through S5 are 1st to 5th yr soybean following 5 yr of corn; Sc# is 2nd (2013) or 1st (2014) yr soybean previously in annual rotation; Ss and Sr are continuous soybean recently with SCN-susceptible and resistant cultivars respectively

* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively.

Table 2.12. *Pratylenchus* population densities as influenced by crop sequences and nematicide application in 2010-2012.

	2010						2011						2012					
	Pi†	‡	Pm		Pf		Pi		Pm		Pf		Pi		Pm		Pf	
Rotation•																		
Cn	288	abc	303	a	280	ab	210	ab	127	abc	263	a	315	a	380	a	232	ab
Cc	305	ab	378	a	271	ab	198	ab	119	abc	202	abc	218	ab	450	a	129	bcd
Cs	130	def	94	bcd	209	bc	79	cde	90	abc	213	abc	197	ef	121	cde	125	abc
C1	15	g	36	def	73	cd	23	e	21	e	48	efg	19	h	17	gh	24	gh
C2	45	ef	20	fg	51	de	60	de	21	e	39	fgh	36	fg	76	cde	86	cd
C3	385	abc	131	abc	389	ab	90	bc	58	bc	120	abcd	79	def	159	bcd	124	de
C4	258	abcd	249	ab	279	ab	211	ab	149	ab	229	abc	141	bcd	291	ab	206	a
C5	493	a	416	a	524	a	168	ab	107	abc	255	ab	194	abc	323	abc	186	ab
S1	663	a	319	ab	288	ab	570	a	192	a	145	abc	203	bc	94	bcd	38	def
S2	233	abc	264	ab	300	ab	191	ab	168	ab	104	cdef	103	cde	47	def	34	efg
S3	90	bcde	48	cde	83	d	149	ab	85	abc	39	defg	79	def	22	efg	20	fg
S4	63	cde	25	ef	49	de	66	bcd	51	cd	25	gh	45	fg	21	fg	10	gh
S5	43	ef	15	g	53	de	21	de	23	de	28	gh	20	gh	8	h	7	hi
Sc	230	abcd	308	a	226	abc	141	b	91	abc	88	bcde	65	abc	65	cde	32	def
Ss	3	g	4	g	28	e	25	e	5	f	13	h	3	i	1	i	1	j
Sr	18	fg	5	g	3	f	2	f	4	f	4	i	1	i	1	i	3	ij
Nematicide																		
Not applied			149		213		133		88		118		104		209	A	143	A
Applied			178		180		147		77		108		110		50	B	14	B
ANOVA (*F* values)																		
Rotation (R)	8.40	**	15.3	**	12.5	**	9.12	**	13.9	**	12.1	**	29.9	**	19.6	**	22.9	**
Nematicide (N)			0.00		0.16		2.02		1.27		0.13		0.70		30.8	**	122.	**
R x N			1.24		0.75		1.00		1.07		0.56		0.89		2.73	**	1.90	*

† Pi, Pm, Pf are mean nematodes/100 cm^3 soil prior to planting; 47 (2010), 46 (2011), or 54 (2012) days after planting; and at harvest respectively.

‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor.

• Cn and Cc are continuous corn with non-*Bt* and *Bt* cultivars respectively since 2010; Cs is corn in annual rotation; C1, C2, C3, C4, and C5 are 1st, 2nd, 3rd, 4th, and 5th yr corn following 5 yr of soybean; S1, S2, S3, S4, and S5 are 1st, 2nd, 3rd, 4th, and 5th yr soybean following 5 yr of corn; Sc is soybean in annual rotation; Ss is continuous SCN-susceptible soybean; and Sr is continuous soybean (SCN-resistant cultivar since 2010). All other soybeanswere SCN-susceptible.

* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively.

Table 2.13. *Pratylenchus* population densities as influenced by crop sequences and nematicide application in 2013-2014.

	2013						2014					
	Pi†	‡	Pm		Pf		Pi		Pm		Pf	
Rotation•												
Cn	733	a	419	abc	451	ab	328	a	180	ab	248	ab
Cc	450	b	284	a	263	ab	165	ab	124	abc	191	abc
Cs#	225	cd	230	abc	356	a	153	e	35	ef	141	bcd
C1	29	efg	37	fg	52	cde	19	ef	14	fg	68	de
C2	98	de	88	bcd	116	bc	37	cde	48	def	37	def
C3	255	c	309	a	239	ab	84	bcd	103	bcd	175	abcd
C4	288	c	319	ab	532	a	146	ab	123	abc	360	a
C5	654	ab	334	ab	586	a	155	ab	224	ab	542	a
S1	528	ab	238	abc	246	ab	369	a	245	a	177	ab
S2	82	ef	57	cde	53	cd	133	bc	137	abc	103	abcd
S3	51	efg	33	efg	47	bc	24	de	58	cde	71	de
S4	58	efg	38	fg	48	def	24	e	51	fg	68	cde
S5	41	fg	11	g	28	efg	27	cde	37	fg	26	efg
Sc#	63	ef	36	def	35	cde	21	ab	140	abc	197	abc
Ss	9	g	1	h	1	g	2	f	4	gh	4	g
Sr	9	g	23	gh	5	fg	2	f	0	h	7	fg
Nematicide												
Not applied	272	A	252	A	347	A	152	A	143	A	234	A
Applied	188	B	59	B	44	B	66	B	51	B	58	B
ANOVA (*F* values)												
Rotation (R)	21.57	**	13.11	**	13.20	**	12.82	**	14.63	**	7.33	**
Nematicide (N)	5.14	*	60.51	**	70.60	**	5.97	*	26.03	**	32.29	**
R x N	1.01		0.97		1.88	*	0.59		0.88		0.77	

† Pi, Pm, Pf are mean nematodes/100 cm^3 soil prior to planting, 64 (2013) or 47 (2014) days after planting, and at harvest respectively.
‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor.
• Cn and Cc are continuous corn recently with non-*Bt* and *Bt* cultivars respectively ; Cs# is 2nd (2013) or 1st (2014) yr corn previously in annual rotation; C1 through C5 are 1st to 5th yr corn after 5 yr of soybean; S1 through S5 are 1st to 5th yr soybean following 5 yr of corn; Sc# is 2nd (2013) or 1st (2014) yr soybean previously in annual rotation; Ss and Sr are continuous soybean recently with SCN-susceptible and resistant cultivars respectively
* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively.

Table 2.14. *Pratylenchus* population densities as influenced by crop sequences with or without nematicide application.

	2012 Pm‡				2012 Pf				2013 Pf			
	Nematicide		No Nematicide		Nematicide		No Nematicide		Nematicide		No Nematicide	
Rotation•												
Cn	138	a	623	ab	14	abcd	244	a	36	abcd	867	a
Cc	96	abc	803	a	23	bcde	442	ab	86	abc	440	ab
Cs#	75	abcdef	167	de	37	abc	212	abcd	142	a	571	a
C1	15	efg	19	e	3	fg	45	fgh	13	abcde	91	de
C2	25	cdef	127	de	12	def	160	bcd	11	bcde	221	abc
C3	32	cdefg	285	cde	11	efg	238	abc	44	abc	434	ab
C4	144	ab	437	bcd	47	a	365	ab	91	a	972	a
C5	68	abcde	578	abc	37	ab	335	ab	93	a	1078	a
S1	55	abcde	133	de	14	cdef	62	cde	83	ab	409	ab
S2	38	bcdef	56	e	6	efg	62	defg	21	cde	85	bcd
S3	18	defg	26	e	4	efg	36	efgh	29	abc	65	cd
S4	13	fg	29	e	5	efg	15	hi	4	e	93	cde
S5	11	gh	6	e	1	g	14	gh	23	de	33	ef
Sc#	67	abcd	62	e	17	bcde	48	cdef	9	de	62	bcd
Ss	1	hi	1	e	1	g	1	j	3	e	0	g
Sr	2	i	0	e	1	g	5	ij	4	de	5	fg
ANOVA (F values)												
Rotation (R)	7.92	**	5.50	**	6.11	**	13.53	**	11.99	**	4.03	**

† Pi, Pm, Pf are mean population densities (nematodes per 100 cm3 soil) prior to planting; 47 (2010), 46 (2011), or 54 (2012) days after planting; and at harvest respectively.

‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor.

• Reflects most recent crop (previous season for Pi). Cn is continuous corn with non-*Bt* cultivar; Cc is continuous corn recently with *Bt* cultivar; Cs#, corn in annual rotation except 2013 which is 2nd yr corn previously in annual rotation; C1, C2, C3, C4, and C5 are 1st, 2nd, 3rd, 4th, and 5th yr corn following 5 yr of soybean; S1, S2, S3, S4, and S5 are 1st, 2nd, 3rd, 4th, and 5th yr soybean following 5 yr of corn; Sc#, soybean in annual rotation except 2013 which is 2nd yr soybean previously in annual rotation; Ss continuous SCN-susceptible soybean; Sr, continuous soybean recently with SCN-resistant cultivar. All soybeans, except Sr, were SCN-susceptible.

* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively.

In most seasons, *Pratylenchus* populations were smallest in long-term soybean monoculture (Ss and Sr) and near minimum detectable levels. In these seasons, population densities decreased significantly throughout the length of soybean monoculture tested, although not necessarily incrementally by year (Tables 2.12 and 2.13). *Pratylenchus* populations did reach minimums following 5 years of soybean in spring 2010, midseason 2010, and spring 2011; and did not change significantly with further increases in years in soybean.

Pratylenchus populations were significantly different in annual rotation compared to 10-year rotation in a few instances. *Pratylenchus* populations before planting or in 1st year of corn were significantly greater following 1 than 5 years of soybean in most seasons from 2010 to spring 2013. In contrast, in most seasons, *Pratylenchus* populations were similar following 1 or 5 years of corn when comparing sequences in soybean for the same length. In spring 2011 and 2013, population densities were significantly greater following 5 years than 1 year in corn.

In midseason 2012, fall 2012, and fall 2013, there were significant crop sequence by nematicide interactions (Tables 2.12 and 2.13), and there were significant crop sequence effects both with and without nematicide application in all three seasons (Table 2.14). In all three seasons, both with and without nematicide, *Pratylenchus* soil populations generally increased in corn monoculture and decreased in soybean monoculture. With nematicide, across sequences, populations were less than 145 nematodes/100 cm^3 soil- a level unlike to affect yield. Population densities were more similar across crop sequences with nematicide than without nematicide application.

3.6 *Helicotylenchus*

Nematicide applications significantly decreased *Helicotylenchus* soil populations in fall 2010 and 2011, midseason and fall 2012, and every season in 2013 and 2014 compared to no nematicide application (Tables 2.15 and 2.16). Terbufos nematicide (fall 2010 and 2011) reduced *Helicotylenchus* populations 33% and 20% compared to no nematicide application. Aldicarb nematicide reduced *Helicotylenchus* 52%, 75%, and 76% in midseason 2012-2014; 87%, 87%, and 78% in fall 2012-2014; and 43% and 73% in spring 2013 and 2014 respectively compared to no nematicide application.

There were significant crop sequence effects on *Helicotylenchus* populations in every season except spring 2013 (Tables 2.15 and 2.16). In some seasons, population densities were significantly greater in or following extended corn (4 or more years) than

extended soybean monoculture (2010, spring 2011, midseason and fall 2013, midseason and fall 2014). In other seasons, population densities were significantly greater in long-term corn monoculture (Cc and Cn) than most other crop sequences (fall 2011), significantly smaller in or following extended (4 or more years) soybean monoculture than most other crop sequences (spring 2014) or both (midseason 2011, spring 2012, and midseason 2012).

In fall 2012, there was crop sequence by nematicide interaction (Table 2.15) with significant crop sequence effects only without nematicide (Table 2.17). Without nematicide, *Helicotylenchus* population was greater under C3 and C4 than any other sequence and smaller under Ss, Sr, and S5 than many other sequences.

3.7 *Xiphinema*

Overall, *Xiphinema* soil populations were small at the site, averaging 8 nematodes/100 cm^3 soil across plots and seasons. Nematicide applications significantly decreased *Xiphinema* soil populations compared to no nematicide application in all seasons from midseason 2012 through fall 2014 except spring 2014 (Tables 2.18 and 2.19). Nematicide applications significantly increased *Xiphinema* population in fall 2011.

In midseason 2010, fall 2011, and every season in 2012, there were significant crop sequence effects (Table 2.18), but there were no crop sequence effects in 2013 or 2014 (Table 2.19). When there were significant crop sequence effects, *Xiphinema* populations were greater in some sequences in corn monoculture than certain other other sequences. There was also crop sequence by nematicide interaction in spring 2012 (Table 2.18) with significant crop sequence effects only without nematicide application (Table 2.17). Without nematicide application in spring 2012, *Xiphinema* population was greatest in sequences with extended corn monoculture history and undetected in sequences following 5 or more years of soybean.

Table 2.15. *Helicotylenchus* population densities as influenced by crop sequences and nematicide application in 2010-2012.

	2010						2011						2012					
	Pi†	‡	Pm		Pf		Pi		Pm		Pf		Pi		Pm		Pf	
Rotation•																		
Cn	233	abc	716	a	1675	ab	656	a	508	a	1296	a	696	a	648	ab	702	ab
Cc	550	a	849	a	2431	a	923	a	460	a	1222	a	616	a	680	a	597	a
Cs#	215	bcde	241	ab	878	bc	58	efg	76	cd	405	b	87	bcd	258	abc	331	ab
C1	45	de	110	bc	508	cd	181	cd	129	bc	473	b	47	de	99	cd	111	abc
C2	73	de	111	bc	495	cd	150	cde	144	bc	488	b	111	bcd	235	abc	268	abc
C3	180	abcd	258	ab	1160	bc	253	c	166	bc	444	b	173	bc	207	c	295	abc
C4	333	abc	250	ab	940	bc	270	c	459	ab	628	b	134	bcd	168	cd	267	abc
C5	185	abcd	310	ab	685	bc	310	bc	158	bc	573	b	96	cde	212	cd	280	abc
S1	278	abc	259	ab	534	cd	304	bc	181	bc	574	b	175	bcd	257	abc	318	ab
S2	335	ab	796	a	1386	ab	264	c	187	abc	513	b	106	bcd	120	cd	159	bc
S3	110	abcde	143	b	445	cd	609	ab	257	ab	650	b	107	bcd	166	bc	172	abc
S4	150	abcd	125	b	201	de	135	cdef	212	abc	191	b	238	b	191	bc	142	abc
S5	118	cde	151	bc	355	cd	90	def	72	cd	202	b	63	de	83	cd	65	cd
Sc#	123	abcd	140	b	278	d	270	cd	212	abc	539	b	133	bcd	138	cd	127	bc
Ss	28	e	98	cd	246	de	73	fg	79	de	214	b	46	ef	70	de	58	de
Sr	8	f	18	d	98	e	20	g	22	e	217	b	20	f	32	e	42	e
Nematicide																		
Not applied			283		937	A	271		220		604	A	199		300	A	434	A
Applied			289		623	B	307		193		482	B	157		145	B	57	B
ANOVA (*F* values)																		
Rotation (R)	5.23	**	5.61	**	6.33	**	9.28	**	4.26	**	3.40	**	7.22	**	4.18	**	3.96	**
Nematicide (N)			0.81		11.4	**	1.33		1.89		4.02	*	0.39		25.7	**	329	**
R x N			0.65		1.54		0.25		1.00		1.80		1.29		1.18		2.12	*

† Pi, Pm, and Pf are mean nematodes/100 cm^3 soil prior to planting; 47 (2010), 46 (2011), or 54 (2012) days after planting; and at harvest respectively.
‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor.
• Cn and Cc are continuous corn with non-*Bt* and *Bt* cultivars respectively since 2010; Cs is corn in annual rotation; C1, C2, C3, C4, and C5 are 1st, 2nd, 3rd, 4th, and 5th yr corn following 5 yr of soybean; S1, S2, S3, S4, and S5 are 1st, 2nd, 3rd, 4th, and 5th yr soybean following 5 yr of corn; Sc is soybean in annual rotation; Ss is continuous SCN-susceptible soybean; and Sr is continuous soybean (SCN-resistant cultivar since 2010). All soybeans, except Sr, were SCN-susceptible.
* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively.

Table 2.16. *Helicotylenchus* population densities as influenced by crop sequences and nematicide application in 2013-2014.

	2013						2014					
	Pi†	‡	Pm		Pf		Pi		Pm		Pf	
Rotation•												
Cn	315		245	a	379	ab	146	abcd	93	abc	163	ab
Cc	298		121	ab	298	a	94	a	134	a	182	abc
Cs#	82		98	ab	195	ab	81	bcde	14	def	90	bcd
C1	28		39	bcd	141	abc	30	abcde	17	cde	83	abc
C2	62		81	abc	109	abc	81	a	25	cdef	118	abc
C3	123		189	ab	266	a	37	cde	72	abc	111	abcd
C4	90		116	abc	352	a	66	ab	59	ab	256	a
C5	81		109	abc	306	ab	93	ab	133	a	179	abc
S1	114		45	bcd	199	abc	59	a	71	abc	162	ab
S2	91		92	ab	132	abc	80	abc	72	bcde	178	abc
S3	105		111	ab	125	abc	33	abcd	32	abcde	43	cd
S4	84		63	abc	144	cd	52	abc	55	abcd	55	cd
S5	93		25	cd	89	abc	40	abcde	49	ef	70	cd
Sc#	89		34	cd	67	bcd	22	abcd	59	abcd	184	abc
Ss	44		17	d	39	d	8	e	11	f	26	d
Sr	22		54	abcd	136	abc	5	de	21	abcde	90	abc
Nematicide												
Not applied	141	A	145	A	328	A	93	A	95	A	199	A
Applied	80	B	36	B	43	B	25	B	22	B	44	B
ANOVA (*F* values)												
Rotation (R)	1.64		3.08	**	2.61	**	2.51	**	3.15	**	2.13	*
Nematicide (N)	8.36	**	43.31	**	94.17	**	11.84	**	31.06	**	60.06	**
R x N	0.53		0.99		1.29		1.41		1.26		1.09	

† Pi, Pm, Pf are mean nematodes per 100 cm^3 soil prior to planting, 64 (2013) or 47 (2014) days after planting, and at harvest respectively.

‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor.
• Cn and Cc are continuous corn recently with non-*Bt* and *Bt* cultivars respectively ; Cs# is 2nd (2013) or 1st (2014) yr corn previously in annual rotation; C1 through C5 are 1st to 5th yr corn after 5 yr of soybean; S1 through S5 are 1st to 5th yr soybean following 5 yr of corn; Sc# is 2nd (2013) or 1st (2014) yr soybean previously in annual rotation; Ss and Sr are continuous soybean recently with SCN-susceptible and resistant cultivars respectively.
* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively.

Table 2.17. *Xiphinema* and *Helicotylenchus* population densities as influenced by crop sequences with or without nematicide application in 2012.

	Nematicide			
	Helicotylenchus		*Xiphine*ma	
	Pf†	‡	Pi	
ANOVA (F values)				
Rotation (R)	1.06		1.64	
	No nematicide			
Rotation•				
Cn	175	bcd	2	bcd
Cc	492	b	5	abc
Cs	524	b	1	cd
C1	437	bc	0	d
C2	499	bc	5	ab
C3	1115	a	16	a
C4	1296	a	6	ab
C5	526	b	16	a
S1	560	b	1	cd
S2	293	bcd	1	cd
S3	316	bcd	2	bcd
S4	203	bcd	4	bcd
S5	109	cd	7	ab
Sc	222	bcd	9	ab
Ss	83	d	0	d
Sr	101	d	0	d
ANOVA (F values)				
Rotation (R)	4.38	**	4.56	**

† Pi, Pm, Pf are mean population densities (nematodes per 100 cm^3 soil) prior to planting; 47 (2010), 46 (2011), or 54 (2012) days after planting; and at harvest respectively.
‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor.
• Cn is continuous corn with non-*Bt* cultivar; Cc is continuous corn recently with *Bt* cultivar; Cs, corn in annual rotation with soybean; C1, C2, C3, C4, and C5 are 1st, 2nd, 3rd, 4th, and 5th yr corn following 5 yr of soybean; S1, S2, S3, S4, and S5 are 1st, 2nd, 3rd, 4th, and 5th yr soybean following 5 yr of corn; Sc, soybean in annual rotation with corn; Ss continuous SCN-susceptible soybean; Sr, continuous soybean recently with SCN-resistant cultivar. All soybeans, except Sr, were SCN-susceptible.
* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively.

Table 2.18. *Xiphinema* population densities as influenced by crop sequences and nematicide application in 2010-2012.

	2010				2011				2012					
	Pi†	Pm	‡	Pf	Pi	Pm	Pf		Pi		Pm		Pf	
Rotation•														
Cn	0	4	bc	8	5	2	10	ab	10	abc	12	a	14	bcd
Cc	8	11	ab	36	8	3	13	a	16	a	8	abc	18	ab
Cs#	8	0	c	10	3	1	5	abcd	0	cd	11	ab	6	d
C1	3	0	c	1	1	2	6	abcd	2	cd	4	bcd	7	cd
C2	5	1	c	5	3	2	5	abcde	3	bcd	3	cd	6	d
C3	3	3	bc	29	3	1	6	abc	7	bcd	5	bcd	13	bcd
C4	23	5	bc	19	4	2	7	abc	4	bcd	6	abc	13	abcd
C5	8	11	a	20	5	3	15	a	11	ab	10	abc	18	a
S1	10	3	bc	10	6	3	11	ab	4	bcd	7	abc	11	bcd
S2	3	9	abc	14	4	2	2	cde	4	bcd	8	abc	7	cd
S3	3	1	c	4	4	2	3	bcde	2	cd	12	ab	13	abc
S4	3	4	bc	4	3	1	4	abcde	7	bcd	9	abc	8	cd
S5	3	1	c	4	1	1	2	cde	1	d	4	abc	3	d
Sc#	13	1	c	0	4	1	4	abcde	2	d	6	abc	7	cd
Ss	0	1	c	0	1	0	1	de	0	d	4	abc	2	d
Sr	3	0	c	0	0	1	0	e	0	d	0	d	3	d
Nematicide														
Not applied		3		11	4	1	4	B	5		10	A	16	A
Applied		4		10	3	2	7	A	5		4	B	2	B
ANOVA (*F* values)														
Rotation (R)	0.81	1.90	*	1.30	1.27	0.57	2.38	*	2.26	*	2.25	*	2.35	*
Nematicide (N)		0.96		0.78	0.96	0.38	3.97	*	0.00		60.8	**	120	**
R x N		0.84		1.36	1.50	1.28	1.21		1.88	*	1.77		1.14	

† Pi, Pm, Pf are mean nematodes per 100 cm^3 soil prior to planting; 47 (2010), 46 (2011), or 54 (2012) days after planting; and at harvest respectively.
‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor.
• Cn and Cc are continuous corn with non-*Bt* and *Bt* cultivars respectively since 2010; Cs is corn in annual rotation; C1, C2, C3, C4, and C5 are 1st, 2nd, 3rd, 4th, and 5th yr corn following 5 yr of soybean; S1, S2, S3, S4, and S5 are 1st, 2nd, 3rd, 4th, and 5th yr soybean following 5 yr of corn; Sc is soybean in annual rotation; Ss is continuous SCN-susceptible soybean; and Sr is continuous soybean (SCN-resistant cultivar since 2010).
* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively.

Table 2.19. *Xiphinema* population densities as influenced by crop sequences and nematicide application in 2013-2014.

	2013						2014					
	Pi†		Pm		Pf		Pi	Pm		Pf		
Nematicide												
Not applied	4	A	7	A	5	A	1	2	A	2	A	
Applied	2	B	2	B	0	B	1	0	B	0	B	
ANOVA (*F* values)												
Rotation (R)	0.63		1.35		0.80		1.37	1.23		0.54		
Nematicide (N)	7.29	**	4.93	*	15.54	**	0.80	5.03	*	4.82	*	
R x N	1.02		1.53		0.84		0.60	1.17		0.71		

† Pi, Pm, Pf are mean nematodes per 100 cm^3 soil prior to planting, 64 (2013) or 47 (2014) days after planting, and at harvest respectively.
‡ Values followed by different letters in the same column are significantly different based on ANOVA.
* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively.

4. Discussion

Aldicarb nematicide applications were effective for increasing soybean yields in 2 of 3 years (2012 & 2013) it was applied, but terbufos nematicide was not effective. Aldicarb is not registered for use on corn or soybean in the Midwestern United States and the aldicarb formulation tested in this study is being phased out, so these nematicides are not an option for nematode management on soybeans at this time. Aldicarb nematicide applications effectively reduced SCN egg and vermiform populations in a few seasons, but this was not consistent across seasons. SCN egg and vermiform populations were reduced in at least one season of each year that nematicide increased soybean yield (2012 and 2013), however, nematicide effect on SCN was generally detected only in fall, while early-season SCN has the most influence on yield (Schmitt et al., 1987; Chen et al., 2001b). Additionally, nematicide reduced SCN populations in midseason of 2011 (eggs) and 2014 (vermiform nematodes) when nematicide did not affect soybean yield suggesting reduction in SCN populations with nematicide was not enough to affect yield in those years.

While inconsistent correspondence of reduced SCN population and increased soybean yield provided weak evidence that SCN influenced soybean yield in this study, the negative impact of SCN on soybean yield is well-documented (Niblack et al., 1992; Chen et al., 2001a; Chen et al., 2001b; Koenning and Wrather, 2010; Rotundo et al., 2010). Additionally, aldicarb has successfully reduced SCN populations in studies in the Midwest (Noel, 1987; Smith et al., 1991; Niblack et al., 1992) although it was ineffective

in one study (Rotundo et al., 2010) and in no study was it effective in all instances. Nematicide applications were less effective against SCN than other plant-parasitic nematodes at the site. Cyst structures may have protected SCN from some effects of nematicide (Inagaki and Tsutsumi, 1971), although vermiform SCN stages, not protected by cyst structure, would come in contact with the nematicide upon entry into the soil or root penetration as aldicarb is a systemic nematicide (Smith et al., 1991).

Aldicarb nematicide applications consistently increased corn yields, but terbufos was not effective which corresponded with the relative effectiveness of the two nematicides against *Pratylenchus* and *Xiphinema*. Aldicarb was effective against *Helicotylenchus,* and terbufos was effective against *Helicotylenchus* in some instances. Efficacy of aldicarb against these nematodes has been demonstrated elsewhere as aldicarb reduced *Pratylenchus* and *Xiphinema* populations 70-90%, and *Helicotylenchus* population 50% in an Iowa study across various sites (Norton et al., 1978). In the same Iowa study, terbufos—at rate half that used in the present study--reduced *Pratylenchus* population 79% (Norton et al., 1978) compared to 20-33% in this study.

In the present study, decreases in *Helicotylenchus* under terbufos nematicide did not correspond to yield increase which may be because *Helicotylenchus* is only damaging with large populations (Norton et al., 1978; Niblack, 1992; Kinloch, 1998; Windham, 1998) or because differences in population occurred in fall, after most plant damage occurs. Plant-parasitic nematode population decreases did correspond with corn yield increases in most cases, most notably for *Pratylenchus*, suggesting that plant-parasitic nematodes affected corn yield in this study. *Xiphinema* population was small, making it unlikely that control of this nematode contributed to corn yield increase. Decreases in both *Helicotylenchus* and *Pratylenchus* populations under aldicarb nematicide application were substantial suggesting either nematode may have affected corn yield. Evidence from other research suggests *Helicotylenchus* only causes minor yield loss, and only at very large populations (Norton et al., 1978; Niblack, 1992; Kinloch, 1998; Windham, 1998), so it is unlikely that *Helicotylenchus* was the main cause of yield loss without nematicide application. *Pratylenchus* is known to cause substantial yield loss (Norton and Hinz, 1976; Norton et al., 1978; Norton, 1984; Todd and Oakley, 1996) and overall nematicide efficacy across crop sequences against *Pratylenchus* corresponded closely to efficacy increasing corn yield. This suggests *Pratylenchus* control may have contributed to corn yield increases of 3-9% with nematicide

applications. However, yield increase with aldicarb nematicide cannot be attributed solely to nematode control with certainty because aldicarb has other effects. Aldicarb also affects insects (Todd and Canerday, 1972; Herbert et al., 1987). While *Bt* corn was used to minimize insect impact, insect control could have contributed to yield benefits of nematicide application. Additionally, under certain environmental conditions, aldicarb may increase plant growth in the absence of disease pressure (Barker et al., 1988).

The benefit of rotation with corn for SCN management was clearly demonstrated by the strong influence of crop sequences on SCN populations. The increase in SCN population in early years of soybean monoculture, but subsequent leveling off of SCN populations, particularly egg populations, with extended soybean monoculture suggests SCN populations reached carrying capacities in that field for the given season. Additionally, maximum populations under soybean monoculture varied by year, which could be considered a change in carrying capacity of that field based on conditions in that growing season such as soybean cultivar, soil moisture, temperature, and soybean growth. Previous research at the Waseca site where the present study was conducted and a partner site in Lamberton showed a similar increase in SCN egg population under extended soybean monoculture, although maximum population was greater at Lamberton (Porter et al., 2001). In previous research at the site of the present study, SCN 2nd stage juvenile population increase and decrease under soybean and corn monoculture respectively was similar to results of the present study (Chen and Reese, 1999). The rapid increases in SCN population in the first few years of soybean monoculture in many years suggest even 2 or 3 years of SCN-susceptible soybean monoculture can cause long-term SCN problems.

A long non-host phase, in this case 5 years of corn, was more beneficial for SCN management than a short non-host phase, annual rotation, in the present study and in the previous research at the Waseca and Lamberton long-term rotation sites (Chen and Reese, 1999; Porter et al., 2001). In 10-year rotation, the greatest benefit of rotating with corn occurred in the first few years of corn monoculture. After two to three years of corn monoculture, SCN populations were commonly below 200 eggs/100 cm^3 soil, the damage threshold guideline for SCN (Chen, 2011). This suggests SCN-susceptible soybean could be grown following 3 years of corn at this site with minimal yield impact. In a separate study in Minnesota, a 2 or 3 year period of corn cropping was similar to annual rotation for SCN management and 4 years of corn monoculture did not reduce

SCN populations below damage threshold (Chen et al., 2001b), suggesting optimum crop rotation for SCN management varies depending on location and conditions, including other management practices employed. In particular, nematicide was applied in the present study, decreasing average SCN populations and shortening the length of non-host cropping needed to decrease population densities below damage guideline. This shows the benefits of combining management practices to maximize SCN control.

SCN suppression has been documented at a site in long-term continuous soybean monoculture near the site of the present study (Chen, 2007a; Bao et al., 2010; Bao et al., 2011; Bao et al., 2013). In a few seasons of the present study, SCN populations, particularly vermiform nematodes, were decreased in continuous soybean monoculture compared to maximum population in other sequences. At the nearby site, SCN suppression is attributed in part to fungal antagonists of SCN (Chen, 2007a; Bao et al., 2010; Bao et al., 2011; Bao et al., 2013), and in previous research at the site of the present study, the fungus *Hirsutella rhossiliensis* parasitized 20-30% of SCN juveniles in most soybean monoculture sequences during the growing season (Chen and Reese, 1999). Different antagonist organisms target different SCN stages (Jaffee and Muldoon, 1995; Chen et al., 1996; Chen and Chen, 2002; Chen and Liu, 2005; Noel et al., 2010) which may explain why vermiform SCN populations were decreased under soybean monoculture more frequently than SCN egg populations. However, SCN population reductions under extended soybean monoculture did not occur consistently suggesting this trend does not indicate development of a suppressive soil. Decreased root biomass under soybean monoculture (Nickel et al., 1995), and thus decreased food resources for SCN, is a better explanation for this trend. Management conditions, particularly tillage (Chen, 2007a), are different between the two sites, which may explain the difference in SCN-suppression capacities between the two.

Decreased SCN populations under SCN-resistant compared to SCN-susceptible long-term soybean monoculture show SCN-resistant soybean was effective for managing SCN populations, even after 5 years of monoculture. Other studies have also demonstrated that SCN-resistant cultivars are effective, including after 3 (Chen, 2007b) or 4 years (Chen et al., 2001b) of SCN-resistant soybean monoculture. Development of resistance-breaking SCN populations is a concern when cultivars with the same source of SCN resistance are grown repeatedly (Zheng et al., 2006; Niblack et al., 2008; Kim et

al., 2011), but was not a problem at the site of this study yet, based on continuing efficacy of resistant cultivars.

Rotation with soybean helped manage *Pratylenchus* populations based on declines of *Pratylenchus* populations with soybean monoculture. Additionally, a 5 year soybean period was more beneficial for *Pratylenchus* management than a 1 year soybean period. This is not consistent with the reported host range for *Pratylenchus*, which includes both corn and soybean for most species (Zirakparvar, 1980; Belair et al., 2002; Chen and Tsay, 2006). Additionally, previous research suggested *Pratylenchus* populations developed just as well in corn-soybean rotation (Todd, 1991), and soybean monoculture (Johnson et al., 1975) as corn monoculture albeit in short-term studies. However, since host range may vary by nematode population (Zirakparvar, 1980; Belair et al., 2002; Chen and Tsay, 2006), soybean could be a poor host of the particular *Pratylenchus* population at this site, resulting in reduced *Pratylenchus* population under soybean monoculture.

Alternatively, competition between SCN and *Pratylenchus* on soybean may have caused or contributed to *Pratylenchus* population declines under soybean monoculture. Previous greenhouse experiments suggest *Pratylenchus penetrans* outcompetes SCN on soybean when their initial populations are similar or there is a greater ratio of *P. penetrans* to SCN, but SCN may outcompete *P. penetrans* if the initial ratio is greatly (3:1) in favor of SCN (Melakeberhan and Dey, 2003). However, this competition model (Melakeberhan and Dey, 2003) does not explain *Pratylenchus* population decreases in soybean phases of 10-year rotation as before entering the soybean period, the ratio of *Pratylenchus* to SCN was very great since it followed 5 years of corn monoculture. It is possible that the outcome of competition between the specific SCN and *Pratylenchus* populations at the site or outcomes in field settings over longer periods of time differs from the outcomes in the greenhouse study (Melakeberhan and Dey, 2003). Further research is needed to determine the outcome of SCN-*Pratylenchus* interaction and the cause of *Pratylenchus* population decreases under soybean monoculture in this study.

Corn was a good host for the *Pratylenchus* population at this site based on increased populations under corn monoculture compared with soybean monoculture. This was also suggests *Pratylenchus* may be a problem in corn monoculture which is supported by other results (Johnson et al., 1975; Zirakparvar, 1980; Todd and Oakley,

1996). *Pratylenchus* reached a particular maximum population or carrying capacity after 3 to 5 years of monoculture and although the population and length varied by season.

Long phases of rotation with soybean helped manage *Helicotylenchus* populations based on decreased populations in extended soybean monoculture. Similar to *Pratylenchus*, *Helicotylenchus* has a wide host range that includes both corn and soybean for populations that have been tested (Ferris and Bernard, 1971; McGawley and Chapman, 1983; Windham, 1998). However, *Helicotylenchus,* while common, is considered a minor problem (Niblack, 1992) and its relationship with corn and soybean is not well-studied. Competition with SCN or poor host suitability of soybean for this particular nematode population may be the cause of *Helicotylenchus* population declines under soybean monoculture, but more research would be needed to determine this. In contrast, large *Helicotylenchus* populations in extended corn monoculture suggest corn was a good host for this nematode. While corn supported larger populations of *Xiphinema* than soybean, particularly in extended monoculture, populations were small overall. This suggests site conditions, such as soil type or tillage practices, were not favorable for *Xiphinema* or that neither crop was a good host.

In this study, nearly all corn yield decline under monoculture occurred during the first three years of monoculture. Previous studies have also documented similar trends at the site of the present study and its partner long-term rotation sites in Lamberton, Minnesota and Arlington, Wisconsin that shared the same experimental design (Crookston et al., 1991; Porter et al. 1997) although one study in Arlington saw decreasing yields throughout corn monoculture cycle (Meese et al., 1991). Additionally, in the present study, rotation including a 5-year period of soybean had only minimal, inconsistent benefit for corn yield over annual rotation. Similarly, annual rotation and 10-year rotation had similar impact on corn yield in previous studies (Meese et al., 1991; Porter et al., 1997), although corn yield was greater in 10-year than annual rotation in one study (Crookston et al., 1991).

In contrast to corn, soybean yield monoculture declines were gradual in the present study, not noticeable with single-year increases in length of soybean monoculture, and continued over extended periods of time. In past studies at the Waseca and Lamberton long-term rotation sites (Crookston et al., 1991), the Arlington site (Meese et al., 1991), and another at the Lamberton site (Porter et al., 2001), soybean yields generally declined as length of soybean monoculture increased although

less gradually than in the present study. This varied somewhat by location and environment variation though as in other studies at the long-term rotation sites (Porter et al., 1997; Porter et al. 2001), soybean yield declined in the initial 2 or 3 years of monoculture and leveled off with further increases in years in soybean. In the present study, rotation with 5-year corn period was not consistently more beneficial for soybean yield than rotations with shorter periods of corn. Ten-year rotation was more beneficial for soybean yield than annual rotation in previous studies at Waseca and Lamberton (Crookston et al., 1991; Porter et al., 2001), at Arlington (Meese et al., 1991), and across all three sites (Porter et al., 1997). Additionally, in the present study, using SCN-resistant cultivars in soybean monoculture did not consistently improve soybean yield despite decreasing SCN populations. This may be because SCN populations were generally not large in this study.

Soil properties were monitored in this study to ensure that they were not limiting crop yield. Similarity in soil K, pH, and organic matter across crop sequences suggest that these factors were adequately managed and did not contribute to the corn-soybean rotation effect. Differences in soil nitrate between corn and soybean were the result of nitrogen application to only corn plots. Since soil phosphate was only different between continuous soybean monoculture and most other treatments, this should not have affected crop yield across crop sequences. Soil phosphate was in the high or very high range for most sequences in 2013, based on Minnesota recommendations for corn (Kaiser et al., 2011), but fell into the medium range for some sequences in 2014.

In this study, the role of nematodes in the rotation effect was investigated directly by applying nematicide to minimize differences in nematode populations across crop sequences or reduce populations below damaging levels. Success in minimizing nematode populations would have been indicated by significant nematicide by crop sequence interactions for nematode populations, but there were very few significant interactions. There were nematicide by crop sequence interactions for SCN eggs in spring 2011 and SCN vermiform nematodes in spring 2012, but SCN population still varied across crop sequences with nematicide application substantially enough that it may have affected soybean yield. In fall 2013, nematicide clearly minimized SCN egg and vermiform SCN populations as there were no significant differences across crop sequences with nematicide application although there were without nematicide. This did not correspond to a reduction in differences in yield across crop sequences in 2013, so

there was not direct evidence that SCN had a role in the rotation effect for soybean yield. Soybean is correlated with initial SCN density, not necessarily final SCN density, which may explain this lack of relationship (Schmitt et al., 1987; Chen et al., 2001b). Overall, nematicide applications were not effective enough at minimizing SCN populations across sequences to accurately assess the role of SCN in the rotation yield effect. Additionally, SCN populations were not large at the site, so its impact on yield may have been too small to clearly detect using available methods.

Similarly, there was little direct evidence of the role of plant-parasitic nematodes in the rotation effect for corn yield. In fall 2013, there was crop sequence by nematicide interaction, but *Pratylenchus* populations were generally similar across corn sequences with and without nematicide. In most other years (2010, 2011, 2014), nematicide application did not reduce differences in plant-parasitic nematode populations across corn sequences either. In 2012, nematicide application did reduce differences in *Pratylenchus*, and, to some extent, *Helicotylenchus* and *Xiphinema* populations across crop sequences. While there was nematicide by crop sequence interaction for corn yield in 2012, variability in corn yield across crop sequences was not reduced. This suggests the influence of plant-parasitic nematodes, particularly *Pratylenchus*, on the rotation effect for corn yield was not detectable in this study in 2012. In other years, nematicide applications were not effective enough in minimizing *Pratylenchus* populations across sequences to accurately assess the role of *Pratylenchus* in the rotation yield effect.

There was indirect evidence that plant-parasitic nematodes influenced the rotation effect. Crop rotation influenced SCN populations in this study and others, with SCN populations increasing with soybean monoctulure and decreasing with corn monoculture (Chen et al., 2001b; Porter et al., 2001). Additionally, the negative impact of SCN on soybean yields is well-documented (Schmitt et al., 1987; Chen et al., 2001a; Chen et al., 2001b; Chen, 2007b; De Bruin and Pedersen, 2008). This suggests management of SCN populations may have a role in the rotation effect for soybean yield. Similarly, *Pratylenchus* and *Helicotylenchus* populations increased with corn monoculture and decreased with soybean monoculture and corn yield increases with nematicide application corresponded to decreases in populations of these nematodes. Additionally, *Pratylenchus* is known to cause corn yield loss (Norton and Hinz, 1976; Norton et al., 1978; Norton, 1984; Todd and Oakley, 1996) and *Helicotylenchus* is

correlated with corn yield loss (Norton et al., 1978). This suggests plant-parasitic nematodes may have a role in the rotation effect for corn yield as well.

In summary, this study documented the distinct way different corn-soybean crop sequences influence SCN, *Pratylenchus*, *Helicotylenchus*, and *Xiphinema* populations. Additionally, the benefits of crop rotation for crop yield and the presence of the corn-soybean rotation yield effect were documented in this study. While nematicide application did not directly confirm and quantify the role of plant-parasitic nematodes in the corn-soybean rotation effect, this study provided indirect evidence that plant-parasitic nematodes may play a role in the rotation effect.

Chapter 3

Influence of Long-Term Crop Sequences on Soil Ecology as Indicated by the Nematode Community

1. Introduction

Crop rotation is a common practice in agricultural systems to maintain crop productivity. In the United States, corn-soybean rotation is among the most important agronomic systems and is a major feature of the landscape. In 2014, 37 and 34.3 million hectares of corn and soybean respectively were planted in the United States which is 53.5% of total area planted to principal crops (NASS-USDA, 2014) or 4% of total land area (Nickerson et al., 2011). Most research on corn-soybean rotation has focused on agronomic factors such as crop yield (Crookston and Kurle, 1989; Crookston et al., 1991; Porter et al., 1997; Howard et al., 1998; Wilhelm and Wortmann, 2004), soil nutrients (Peterson and Varvel, 1989; Meese et al., 1991; Omay et al., 1998), pathogen populations (Whiting and Crookston, 1993; Howard et al., 1998; Porter et al., 2001), other soil properties (Meese et al., 1991; Copeland et al., 1993), and plant physiology (Copeland and Crookston, 1992; Nickel et al., 1995; Pikul et al., 2012).

Less is known about the impact of different cropping systems on soil biology and ecology. Since corn-soybean systems are so common, a better understanding of this system would provide a better understanding of our landscape. Additionally, a better understanding of soil ecology under different cropping systems may give insight into mechanisms behind agronomic benefits of crop rotation and help determine optimal practices for maintaining productive soil. The nematode community is a dynamic indicator of soil ecology because it spans a wide range of trophic groups and ecological niches, and is sensitive to changes in the environment (Bongers, 1990; Ferris et al., 2001; Fiscus and Neher, 2002).

The nematode community has been used as a tool for assessing various management practices in agricultural systems including tillage (Sanchez-Moreno et al., 2006; Okada and Harada, 2007; Villenave et al., 2009), fertilizer application (Hu and Cao, 2008; Leroy et al., 2009; Liang et al., 2009; Villenave et al., 2010), and organic management practices (Dong et al., 2008; Overstreet et al., 2010). Only a few studies have examined the influence of different cropping systems on the nematode community (Osler et al., 2000; Govaerts et al., 2006; Rahman et al., 2007; Carter et al., 2009; Briar et al., 2012; Djigal et al., 2012) and none have focused on corn-soybean rotations in a

temperate climate.

Examining distinct cropping sequences over an extended time period may reveal trends that are not apparent over a shorter time period and reflects the long time periods that agricultural fields remain in production. In 1982, a long-term field study involving various corn and soybean crop sequences was initiated in Waseca, Minnesota to examine agronomic aspects of corn-soybean rotation when soil nutrients are not limiting. This site is a unique opportunity to examine the influence of corn-soybean crop rotations on soil ecology and the nematode community.

To help determine the role of nematodes in agronomic aspects of crop rotation, crop sequences with and without nematicide application have been maintained at the site since 2010. In particular, soybean cyst nematode (*Heterodera glycines*) is the major pathogen of soybean in this area, causing yield losses of 30% or more in some cases (Chen et al., 2001). Plant-parasitic nematode population dynamics and other agronomic aspects of the study are reported elsewhere (Chapter 2). Environmental impacts of pesticide application are increasingly under scrutiny with many nematicides no longer approved for use (Rich et al., 2004). Additionally, nematicides can impact both target nematodes that damage plants and non-target nematodes (De Bruin and Pedersen, 2008; Sanchez-Moreno et al., 2010; Chelinho et al., 2011) that provide beneficial services in the soil ecosystem (Ferris et al., 2012) making it important to understand the full impact of these applications. Nematicide can also be a tool to understand the role of nematodes in the impacts of crop rotation on other agronomic factors. Based on this, the objective of this study was to assess impact of nematicide application and long-term crop rotations on soil ecology based on the nematode community.

2. Materials and Methods

2.1 Experimental Design

The study was conducted in a Nicollet clay loam (fine-loamy, mixed, mesic Aquic Hapludoll) at the Southern Research and Outreach Center in Waseca, Minnesota at a field site where plots of various corn-soybean crop sequence treatments have been maintained continuously since 1982. The 16 crop sequences (Table 3.1) were: (i) five years corn followed by 5 years soybean with each phase grown each year such that both crops have treatments in years 1, 2, 3, 4, and 5 of monoculture every year; (ii) annual rotation with both crops planted each year; (iii) continuous monoculture of each crop; (iv) annual rotation between two cultivars--but crop monoculture--of each crop.

Since 1995, sequence (iv) was single-cultivar monoculture of each crop. Beginning in 2010, sequences (i), (ii), and (iii) were soybean susceptible to soybean cyst nematode (SCN) and *Bt* corn while sequence (iv) was SCN-resistant soybean cultivars with PI88788 resistance source and non-*Bt* corn cultivars. Before 2010, all sequences were SCN-susceptible soybean. From 2012-2013, sequence (ii) was not rotated, so crops were planted two years in a row rather than rotated annually and this sequence was removed during later analysis.

Table 3.1. Corn (C) and soybean (S) cropping sequences treatments† at the field site 2005-2014.

	Crop sequence by year									
Treatments	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014
10-year rotation										
1.	C4	C5	S1	S2	S3	S4	S5	C1	C2	C3
2.	C3	C4	C5	S1	S2	S3	S4	S5	C1	C2
3.	C2	C3	C4	C5	S1	S2	S3	S4	S5	C1
4.	C1	C2	C3	C4	C5	S1	S2	S3	S4	S5
5.	S5	C1	C2	C3	C4	C5	S1	S2	S3	S4
6.	S4	S5	C1	C2	C3	C4	C5	S1	S2	S3
7.	S3	S4	S5	C1	C2	C3	C4	C5	S1	S2
8.	S2	S3	S4	S5	C1	C2	C3	C4	C5	S1
9.	S1	S2	S3	S4	S5	C1	C2	C3	C4	C5
10.	C5	S1	S2	S3	S4	S5	C1	C2	C3	C4
Annual rotation										
11.	Sc	Cs	Sc	Cs	Sc	Cs	Sc	Cs	Cs#	Sc#
12.	Cs	Sc	Cs	Sc	Cs	Sc	Cs	Sc	Sc#	Cs#
Continuous Monoculture										
13.	C	C	C	C	C	Cc	Cc	Cc	Cc	Cc
14.	Ss	Ss	Ss	Ss	Ss	Ss	Ss	Ss	Ss	Ss
Continuous; non-*Bt* corn & SCN-resistance soybean post-2010, alternating cultivars pre-1995										
15.	C	C	C	C	C	Cn	Cn	Cn	Cn	Cn
16.	Ss	Ss	Ss	Ss	Ss	Sr	Sr	Sr	Sr	Sr

† Cn and Cc are continuous corn recently (2010-2014) with non-*Bt* and *Bt* cultivars respectively; C is continuous corn; Cs# is 2nd (2013) or 1st (2014) yr corn previously in annual rotation; C1 through C5 are 1st to 5th yr corn after 5 yr of soybean; S1 through S5 are 1st to 5th yr soybean following 5 yr of corn; Sc# is 2nd (2013) or 1st (2014) yr soybean previously in annual rotation; Ss and Sr are continuous soybean recently with SCN-susceptible and resistant cultivars respectively. All soybeans, except Sr, were susceptible to SCN. From 2010-2014, all corn, except Cn, had *Bt* trait.

From 2010 onward, half of each plot was treated with in-furrow, granular nematicide to create a split-plot experiment arrangement with subplots 4.57 m wide by 7.62 m long with 6 crop rows. In 2010 and 2011, terbufos nematicide (Counter 20G, AMVAC Chemical Corporation) was applied in-furrow at planting at 2.44 kg a.i./ha. In

2012 and 2013, aldicarb nematicide (Temik 15G, Bayer Crop Sciences) was applied in-furrow at planting at 2.94 kg a.i./ha. The experiment was a randomized complete block design with 4 replicates.

2.2 Site management

Corn and soybean were planted, with concurrent nematicide applications to appropriate subplots, on June 3, 2013; and May 21, 2014. Corn cultivars planted were De Kalb 50-66 (*Bt*-trait corn sequences) and was DeKalb 50-67 (*Bt*-free corn sequences). Soybean cultivars planted were Pioneer 92Y22 (SCN-susceptible soybean sequences) and Pioneer 92Y12 (SCN-resistant soybean sequences).

Plots were managed with conventional tillage with the site chisel plowed each fall and field cultivated each spring before planting and soil sampling. Weeds and insects were managed with herbicide and insecticide applications as needed. Glyphosate herbicide was applied on June 28, 2013 and June 11, 2014 at 1.14 and 1.42 liters a.i./ha respectively. In 2014, lambda-cyhalothrin foliar insecticide (Warrior, Syngenta Crop Protection Inc.) was applied at 0.028 kg a.i./ha on August 19 for soybean aphid (*Aphis glycines*) control.

Crops were fertilized such that soil nutrients should not have been a limiting factor. Since site establishment, plots planted to corn received nitrogen application above the recommended rate on a yearly basis while P and K were applied every 3 years or more frequently if needed based on soil testing. In 2013 and 2014, plots planted to corn received nitrogen applications at 224 kg N/ha in the form of urea with agrotain. This was surface-broadcast without incorporation on June 12 and June 11 respectively. In 2014, all plots also received P at 78 kg/ha in the form of triple super phosphate and K at 39 kg/ha in the form of potash.

2.3 Soil sampling and nematode assessement

Soil samples for nematode community analysis were collected in 2013 and 2014 at three times during each growing season: spring (2 days or less before planting), midseason, and fall (at harvest) from all subplots. From each subplot, 20 soil cores were taken in the two central rows (within 4 cm of plant rows) to a depth of 15 cm. Soil samples were homogenized by passing through a metal screen with 4 mm apertures before further processing. In 2013, soil samples were collected on June 3, August 6 (64 days after planting [DAP]), and October 8 (127 DAP). In 2014, soil samples were collected on May 19, July 7 (45 DAP), and October 9 (94 DAP).

Table 3.2. Summary of nematode trophic groups and nematode community indices.			
Variable	Symbol	Calculation or summary	Greater value Indicates
herbivores		abundance of nematodes that feed on plants; may or may not cause yield loss	more plant productivity or more plant stress, later stage of succession in certain ecosystems
bacterivores		abundance of nematodes that feed on bacteria	greater bacteria abundance, usually enriched food web
fungivores		abundance of nematodes that feed on fungi	greater fungal abundance, generally more stable food web
omnivores		abundance of nematodes that feed on a variety of food sources	less disturbed system, more trophic links, more structured food web, possibly greater suppression of plant-parasitic nematodes
predators		abundance of nematodes that feed on other nematodes or invertebrates	less disturbed system, more trophic links, more structured food web, possibly greater suppression of plant-parasitic nematodes
Shannon-Weaver diversity Index		(genera relative abundance * *ln*(relative abundance)), summed for all genera	more diverse nematode community (more genera with more similar abundance)
maturity index	MI	average nematode c-p value excluding herbivores	less disturbed soil community, later stage of succession
MI25	MI25	same as MI, but nemas with c-p of 1 excluded	less disturbance—ignoring disturbance from enrichment
plant parasite index	PPI	average herbivore c-p value	more mature, specialized herbivore community; more plant production/diversity;
enrichment index	EI	weighted‡, modified relative abundance of opportunistic nematodes	soil has more food and nutrient resources (enriched condition)
basal index	BI	weighted, modified relative abundance of stress-tolerant nematodes	more environmental stress, fewer resources (basal condition)
structure index	SI	weighted, modified relative abundance of high c-p nematodes	more trophic links (structure); later stage of succession
channel index	CI	weighted ratio of fungivores to bacterivores	decomposition mediated by fungi more than bacteria (more advanced condition)
(F+B)/PP	FBPP	(# fungivores +bacterivores)/# herbivores	more favorable plant growth conditions, more beneficial ecological services
‡ weights give more value to nematodes that are larger (consume more resources) or more strongly representative of the index, (*i.e.*enrichment opportunists have a larger weight in EI)			

Vermiform nematode population density was determined for all soil samples collected at spring, midseason, and fall in 2013 and 2014. Vermiform nematodes from each subplot were extracted from a 100 cm^3 homogenized soil subsample using a modified sucrose floatation and centrifugation method (Jenkins, 1964). Nematode

abundance was calculated based on a subsample of at least 10% of extracted nematode solution. A subsample of at least 100 nematodes from each subplot was identified morphologically to genus using a light microscope and soil population density for vermiform stages of each genus was calculated. Based on this information, abundances (nematodes /100 cm^3 soil) of total nematodes, herbivores, bacterivores, fungivores, omnivores, and predators were calculated. Select nematode community indices were also calculated including Shannon-Weaver diversity index (Neher and Darby, 2009), maturity index (Bongers, 1990), MI25 (Bongers and Korthals, 1993), plant parasite index (Bongers, 1990), enrichment index, basal index, structure index, channel index (Ferris et al., 2001), and FBPP (Wasilewska, 1989). The calculations of these indices and basic interpretation of abundances and indices are summarized in Table 3.2.

2.4. Statistical Analysis

Within each season (spring, midseason, and fall), data was combined across years—combined within treatments--and these combined data were analyzed using two-way, split-plot ANOVA. Annual rotation treatments were removed from this combined data set because the rotation of these treatments was disrupted in 2013 & 2014. ANOVA models were checked for homogeneity of variance using Levene's test and for normality of residuals graphically (Levene, 1960; Cook and Weisburg, 1999). When necessary, response variables were transformed to meet these assumptions (Table 3.2). For variables with significant crop sequence effects ($P \leq 0.05$), crop sequence treatment means were separated using Fischer's protected LSD ($P \leq 0.05$). All analyses were performed using R version 3.0 (The R Foundation for Statistical Computing, Vienna).

3. Results

3.1 Taxonomy and summary statistics

Over 6 seasons in 128 plots, nematodes spanning 64 genera were identified in soil at the site (Table 3.3). Bacterivores were most abundant representing 49.4% of total nematode population across seasons and plots, followed by herbivores (39.1%), fungivores (10.6%), omnivores (0.71%), and predators (0.09%). Among bacterivores, *Rhabditis* was most common, representing 33.9% of total nematode population (relative abundance). Among herbivores, *Filenchus* was most common at 13.3%. *Aphelenchoides* was the most common fungivore at 8.2%. *Thonus* and *Clarkus* were the most common omnivore and predators respectively at 0.26% and 0.06%.

Table 3.3. Nematodes identified at the study site across seasons and plots

Genus	Family	Cp value	Feeding type	Relative abundance†
Bunonema	Bunonematidae	1	Bacterivore	<0.01%
Diplogaster	Diplogasteridae	1	Bacterivore	2.77%
Diploscapter	Diploscapteridae	1	Bacterivore	<0.01%
Mesorhabditis	Rhabditidae	1	Bacterivore	0.53%
Panagrolaimus	Panagrolaimidae	1	Bacterivore	0.82%
Rhabditis	Rhabditidae	1	Bacterivore	33.88%
Acrobeles	Cephalobidae	2	Bacterivore	0.04%
Acrobeloides	Cephalobidae	2	Bacterivore	0.01%
Acrolobus	Cephalobidae	2	Bacterivore	0.05%
Cephalobus	Cephalobidae	2	Bacterivore	5.56%
Cervidellus	Cephalobidae	2	Bacterivore	0.03%
Chiloplacus	Cephalobidae	2	Bacterivore	0.07%
Chronogaster	Leptolaimidae	2	Bacterivore	0.01%
Eucephalobus	Cephalobidae	2	Bacterivore	2.90%
Eumonhystera	Eumonhysteridae	2	Bacterivore	0.54%
Plectus	Plectidae	2	Bacterivore	2.10%
Wilsonema	Plectidae	2	Bacterivore	0.07%
Aulolaimus	Aulolaimidae	3	Bacterivore	<0.01%
Paraphanolaimus	Halaphanolaimidae	3	Bacterivore	<0.01%
Prismatolaimus	Prismatolaimidae	3	Bacterivore	0.01%
Alaimus	Alaimidae	4	Bacterivore	0.07%
Paramphidelus	Alaimidae	4	Bacterivore	0.01%
Aphelenchoides	Aphelenchoididae	2	Fungivore	8.18%
Aphelenchus	Aphelenchidae	2	Fungivore	2.37%
Aprutides	Aphelenchoididae	2	Fungivore	<0.01%
Paraphelenchus	Aphelenchidae	2	Fungivore	0.06%
Diphtherophora	Campydoridae	4	Fungivore	0.01%
Tylencholaimus	Leptonchidae	4	Fungivore	0.01%
Basiria	Tylenchidae	2	Herbivore	0.75%
Boleodorus	Tylenchidae	2	Herbivore	0.02%
Ditylenchus	Anguinidae	2	Herbivore	1.88%
Filenchus	Tylenchidae	2	Herbivore	13.26%
Malenchus	Tylenchidae	2	Herbivore	<0.01%
Paratylenchus	Paratylenchidae	2	Herbivore	0.02%
Psilenchus	Psilenchidae	2	Herbivore	1.28%
Tylenchus	Tylenchidae	2	Herbivore	0.01%
Helicotylenchus	Hoplolaimidae	3	Herbivore	7.05%
Heterodera	Heteroderidae	3	Herbivore	4.37%
Pratylenchus	Pratylenchidae	3	Herbivore	10.20%
Trophurus	Dolichodoridae	3	Herbivore	0.01%
Tylenchorrhynchus	Dolichodoridae	3	Herbivore	0.01%
Pungentus	Nordiidae	4	Herbivore	0.01%
Axonchium	Belondiridae	5	Herbivore	0.06%
Dorylaimellus	Belondiridae	5	Herbivore	<0.01%

† percent of total nematode population across seasons and plots

Table 3.3 continued. Nematodes identified at the study site across seasons and plots

Genus	Family	Cp value	Feeding type	Relative abundance†
Longidorella	Thornenematidae	5	Herbivore	<0.01%
Oxydirus	Belondiridae	5	Herbivore	0.02%
Xiphinema	Longidoridae	5	Herbivore	0.14%
Dorydorella	Qudsianematidae	4	Omnivore	0.08%
Eudorylaimus	Qudsianematidae	4	Omnivore	0.15%
Microdorylaimus	Qudsianematidae	4	Omnivore	0.06%
Prodorylaimus	Dorylaimidae	4	Omnivore	0.01%
Thonus	Qudsianematidae	4	Omnivore	0.26%
Aporcelaimellus	Aporcelaimidae	5	Omnivore	0.11%
Aporcelaimium	Aporcelaimidae	5	Omnivore	<0.01%
Aporcelaimus	Aporcelaimidae	5	Omnivore	<0.01%
Epidorylaimus	Thornenematidae	5	Omnivore	<0.01%
Mesodorylaimus	Thornenematidae	5	Omnivore	0.03%
Tobrilus	Tobrilidae	3	Predator	<0.01%
Trischistoma	Triplylidae	3	Predator	<0.01%
Clarkus	Monochidae	4	Predator	0.06%
Granonchulus	Monochidae	4	Predator	<0.01%
Prionchulus	Monochidae	4	Predator	<0.01%
Discolaimium	Actinolaimidae	5	Predator	0.01%
Discolaimus	Actinolaimidae	5	Predator	0.02%

† percent of total nematode population across seasons and plots

Table 3.4. Bacterivore population densities as influenced by crop sequences and nematicide application for 2013 and 2014 combined.

	Pi†	‡	Pm		Pf	
Rotation•						
Cn	510	de	483	efg	470	e
Cc	446	de	417	fg	421	e
C1	808	ab	580	cdef	592	de
C2	536	cd	663	bcde	530	e
C3	459	de	508	defg	436	e
C4	386	e	366	g	452	e
C5	453	e	475	efg	470	e
S1	474	de	548	cdefg	916	cd
S2	782	ab	729	abc	1154	abc
S3	903	a	889	a	1455	a
S4	899	a	798	ab	1309	ab
S5	670	bc	688	abcd	1364	ab
Ss	752	ab	659	bcde	1244	ab
Sr	959	a	722	abcd	1034	bc
Nematicide						
Not applied	613		654	A	847	
Applied	665		560	B	852	
ANOVA (*F* values)						
Rotation (R)	10.04	**	4.11	**	12.05	**
Year (Y) x R	1.23		1.25		1.08	
Nematicide (N)	2.02		6.48	*	0.01	
Y x N	0.16		0.10		1.57	
R x N	0.89		0.73		0.96	
Y x R x N	1.04		1.18		1.55	

† Pi, Pm, and Pf are mean nematodes/100 cm^3 soil prior to planting, at midseason (64 and 45 days after planting in 2013 & 2014), and at harvest respectively.
‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor (nematicide or rotation).
• Cn and Cc are continuous corn recently (2010-2014) with non-Bt and Bt cultivars respectively; C1 through C5 are 1st to 5th yr corn after 5 yr of soybean; S1 through S5 are 1st to 5th yr soybean following 5 yr of corn; Ss and Sr are continuous soybean recently (2010-2014) with SCN-susceptible and resistant cultivars respectively. All soybeans, except Sr, were SCN-susceptible.

* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively.

3.2 Trophic groups and total nematode populations

3.2.1 Bacterivore population

Bacterivore population was significantly decreased at midseason in treatment with nematicide application compared to treatment without nematicide application (Table 3.4). Bacterivore populations were significantly affected by crop sequence across all three seasons with populations generally significantly greater in soybean than corn (Table 3.4). In particular, before planting, bacterivore populations were significantly greater following soybean than following corn and, in fall, significantly decreased in corn compared to soybean for all sequences. In midseason, bacterivore population was generally significantly greater in soybean than corn, but this varied by crop sequence.

Among soybean sequences, there were few significant differences. Before planting, bacterivore populations were not significantly different across sequences following soybean (Table 3.4). In midseason and fall, bacterivore populations were significantly greater in 3 or more years of soybean monoculture than S1, and significantly smaller in Ss (midseason) or Sr (fall) than S3, but were not significantly different among most other soybean sequences. Among corn sequences, there were also few significant differences (Table 3.4). Before planting, bacterivore populations were significantly greater following 1 than 3 or more years of corn, but were similar among other sequences following corn. In midseason, bacterivore populations were greater in C4 than C1 or C2 and in Cc than C2, but not significantly different among other sequences in corn. In fall, populations were not significantly different across corn sequences.

3.2.2 Fungivore population

Fungivore population was significantly decreased by nematicide application compared to treatment without nematicide application only at midseason (Table 3.5). Fungivore populations were significantly affected by crop sequence in all three seasons with populations significantly increased in corn compared to soybean for most sequences although there was season to season variation (Table 3.5). In particular, in spring fungivore populations were signficantly greater following corn sequences–except following C1— than soybean sequences. In midseason, population densities were generally significantly greater in corn—notably C2 and C3-- than soybean sequences, but this varied by sequence. In fall, population densities were significantly greater in corn—except C1—than soybean sequences.

Among corn sequences, there were few significant variations in fungivore populations. Before planting, population densities were not significantly different following corn for most sequences. In midseason and fall, population densities were significantly smaller in C1 than nearly all other corn sequences and greater in C2 and C3 (midseason) or C3 (fall) than C5. Across seasons, population densities did not vary significantly across most soybean sequences, although density was significantly greater in 1 year than 4 or more years of SCN-susceptible soybean in midseason.

3.2.3 Herbivore population

Nematicide applications significantly decreased herbivore populations in all three seasons compared to treatment without nematicide application (Table 3.6). In both spring and midseason, there were significant crop sequence by nematicide interactions (Table 3.6), and there were significant crop sequence effects for treatment with nematicide application and treatment without nematicide application in both seasons (Table 3.7). In both seasons, there were more significant variations across crop sequences without nematicide than with nematicide application. In spring, with nematicide application, population densities were similar among most sequences, but significantly greater following 4 or more years in corn than some soybean sequences. Without nematicide application, densities were significantly greater in extended corn monoculture than most soybean sequences and significantly increased as length of corn monoculture increased for some contrasts. In midseason with nematicide application, population densities were significantly smaller under Sr and greater under S1 than most other sequences, but not significantly different among most other sequences (Table 3.7). Without nematicide, population densities were significantly smaller under long-term soybean monoculture than most other sequences, but also significantly greater in extended corn monoculture (C5,Cc, and Cn) than most soybean sequences.

In fall, there were significant crop sequence effects (Table 3.6) and herbivore populations were significantly greater in extended corn monoculture (3 or more years) than all soybean sequences except 1st year soybean. Population densities also increased significantly as years in corn increased, from 2 to 4 years of monoculture, but was similar among sequences in 4 or more years of *Bt* corn. Population densities were similar among sequences in soybean 2 to 5 years, but smaller in Ss and larger in S1 than most other soybean sequences.

Table 3.5. Fungivore population densities as influenced by crop sequences and nematicide application for 2013 and 2014 combined.

	Pi†	‡	Pm		Pf	
Rotation•						
Cn	125	ab	138	ab	412	ab
Cc	148	a	125	abc	408	ab
C1	73	cd	54	d	204	cd
C2	99	bc	169	a	381	ab
C3	142	ab	175	a	523	a
C4	144	a	125	ab	352	ab
C5	132	ab	98	bc	305	bc
S1	117	ab	112	bc	195	de
S2	74	cd	73	cd	189	defg
S3	57	d	71	cd	151	fg
S4	66	d	49	d	114	g
S5	59	d	63	d	159	def
Ss	73	cd	64	d	156	efg
Sr	87	cd	71	bcd	153	defg
Nematicide						
Not applied	108		123	A	276	
Applied	92		76	B	254	
ANOVA (*F* values)						
Rotation (R)	7.40	**	5.28	**	13.39	**
Year (Y) x R	0.93		0.67		1.27	
Nematicide (N)	3.42		31.06	**	1.07	
Y x N	0.10		1.09		0.21	
R x N	0.97		1.73		1.01	
Y x R x N	1.40		0.63		0.87	

† Pi, Pm, and Pf are mean nematodes/100 cm^3 soil prior to planting, at midseason (64 and 45 days after planting in 2013 & 2014), and at harvest respectively.

‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor (nematicide or rotation).

• Cn and Cc are continuous corn recently (2010-2014) with non-Bt and Bt cultivars respectively; C1 through C5 are 1st to 5th yr corn after 5 yr of soybean; S1 through S5 are 1st to 5th yr soybean following 5 yr of corn; Ss and Sr are continuous soybean recently (2010-2014) with SCN-susceptible and resistant cultivars respectively. All soybeans, except Sr, were SCN-susceptible.

* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively

Table 3.6. Herbivore population densities as influenced by crop sequences and nematicide application for 2013 and 2014 combined.

	Pi†	‡	Pm		Pf	
Rotation•						
Cn	1002	a	884	a	1023	bc
Cc	745	abc	719	ab	1092	abc
C1	396	def	258	g	419	de
C2	290	f	421	bcde	505	d
C3	406	ef	679	abcd	843	c
C4	517	cd	641	abc	1283	ab
C5	748	bc	807	a	1482	a
S1	781	ab	783	a	1013	abc
S2	389	def	377	defg	518	d
S3	347	def	382	def	459	de
S4	424	def	395	cdef	425	def
S5	446	de	301	fg	393	de
Ss	295	ef	273	efg	279	f
Sr	118	g	209	h	338	ef
Nematicide						
Not applied	623	A	751	A	1122	A
Applied	383	B	283	B	338	B
ANOVA (*F* values)						
Rotation (R)	13.83	**	9.21	**	19.68	**
Year (Y) x R	0.97		1.55		1.17	
Nematicide (N)	52.49	**	131.56	**	235.99	**
Y x N	3.82	*	0.48		8.18	**
R x N	3.90	**	3.07	**	1.32	
Y x R x N	1.63		1.00		0.86	

† Pi, Pm, and Pf are mean nematodes/100 cm^3 soil prior to planting, at midseason (64 and 45 days after planting in 2013 & 2014), and at harvest respectively.
‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor (nematicide or rotation).
• Cn and Cc are continuous corn recently (2010-2014) with non-Bt and Bt cultivars respectively; C1 through C5 are 1st to 5th yr corn after 5 yr of soybean; S1 through S5 are 1st to 5th yr soybean following 5 yr of corn; Ss and Sr are continuous soybean recently (2010-2014) with SCN-susceptible and resistant cultivars respectively. All soybeans, except Sr, were SCN-susceptible.

* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively

Table 3.7. Herbivore and total nematode population densities as influenced by crop sequences with or without nematicide application for 2013 and 2014 combined.

	# Total Nematodes					
	Pi		Pm		Pf	
	Nematicide	No Nematicide	Nematicide	No Nematicide	Nematicide	No nematicide
Rotation•						
Cn	1346	1956	820	2233 a	1115 cd	2707 bc
Cc	1091	1594	761	1794 abc	1315 bcd	2549 bcde
C1	1440	1134	887	925 d	979 d	1458 f
C2	1018	838	998	1539 bcd	1034 cd	1822 def
C3	837	1195	1008	1761 abc	1409 abcd	2211 bcdef
C4	904	1220	722	1559 bcd	1383 abcd	2813 ab
C5	945	1748	771	2016 ab	995 d	3544 a
S1	1118	1644	1340	1580 bcd	1598 abcd	2668 bcd
S2	1176	1328	1060	1335 cd	1669 abc	2074 bcdef
S3	1247	1392	1042	1684 abc	1999 a	2151 bcdef
S4	1318	1483	1020	1492 bcd	1747 ab	1967 cdef
S5	1144	1228	752	1383 bcd	1763 ab	2086 bcdef
Ss	1244	1021	1021	1000 d	1764 ab	1611 f
Sr	1310	1025	789	1231 cd	1415 abcd	1660 ef
ANOVA (*F* values)						
Rotation (R)	0.86	1.73	1.08	2.36 **	2.17 *	3.77 **

	# Herbivores			
	Pi		Pm	
	Nematicide	No Nematicide	Nematicide	No Nematicide
Rotation•				
Cn	678 a	1325 a	320 ab	1448 a
Cc	552 abc	938 abc	338 abc	1100 ab
C1	445 abcd	347 efg	258 bc	257 h
C2	335 bcde	245 g	233 bc	608 bcde
C3	248 ef	565 cde	374 bc	984 abc
C4	323 bcde	711 bcd	306 ab	975 abc
C5	505 abcd	990 abc	284 bc	1330 a
S1	551 ab	1011 ab	591 a	975 abcd
S2	305 cde	472 def	239 bc	515 def
S3	305 cde	388 efg	226 bc	537 cde
S4	266 de	581 cde	220 bc	570 cde
S5	353 bcde	538 de	167 c	435 efg
Ss	301 bcde	290 fg	263 bc	284 gh
Sr	131 f	106 h	92 d	326 fgh
ANOVA (*F* values)				
Rotation (R)	3.54 **	10.1 **	2.94 **	9.03 **

† Pi, Pm, and Pf are mean populations prior to planting, at midseason, and at harvest respectively.
‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$)
• Cn and Cc are continuous corn recently (2010-2014) with non-Bt and Bt cultivars respectively; C1 through C5 are 1st to 5th yr corn after 5 yr of soybean; S1 through S5 are 1st to 5th yr soybean following 5 yr of corn; Ss and Sr are continuous soybean recently (2010-2014) with SCN-susceptible and resistant cultivars respectively.
* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively

Table 3.8. Total nematode population densities as influenced by crop sequences and nematicide application for 2013 and 2014 combined.

	Pi†	‡	Pm		Pf	
Rotation•						
Cn	1651	a	1527		1911	ab
Cc	1342	abc	1278		1932	a
C1	1287	abc	906		1219	c
C2	928	e	1268		1428	bc
C3	1016	de	1385		1810	ab
C4	1062	cde	1140		2098	a
C5	1346	bcd	1393		2269	a
S1	1381	ab	1460		2133	a
S2	1252	bcd	1197		1871	a
S3	1320	abc	1363		2075	a
S4	1401	ab	1256		1857	ab
S5	1186	bcde	1067		1924	a
Ss	1132	bcde	1010		1687	ab
Sr	1167	bcde	1010		1537	abc
Nematicide						
Not applied	1356	A	1549	A	2258	A
Applied	1148	B	931	B	1449	B
ANOVA (*F* values)						
Rotation (R)	3.39	**	1.44		2.89	**
Year (Y) x R	1.62		1.36		1.35	
Nematicide (N)	9.60	**	67.35	**	70.78	**
Y x N	0.43		0.44		1.60	
R x N	2.33	*	2.64	**	3.09	**
Y x R x N	0.47		1.13		1.11	

† Pi, Pm, and Pf are mean nematodes/100 cm^3 soil prior to planting, at midseason (64 and 45 days after planting in 2013 & 2014), and at harvest respectively.
‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor (nematicide or rotation).
• Cn and Cc are continuous corn recently (2010-2014) with non-Bt and Bt cultivars respectively; C1 through C5 are 1st to 5th yr corn after 5 yr of soybean; S1 through S5 are 1st to 5th yr soybean following 5 yr of corn; Ss and Sr are continuous soybean recently (2010-2014) with SCN-susceptible and resistant cultivars respectively. All soybeans, except Sr, were SCN-susceptible.

* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively

Table 3.9. The Shannon-Weaver diversity index as influenced by crop sequences and nematicide application for 2013 and 2014 combined.

	Vi†	‡	Vm		Vf	
Rotation•						
Cn	1.91	ab	1.87	ab	1.77	
Cc	1.93	ab	1.88	a	1.71	
C1	1.70	cd	1.64	bcd	1.89	
C2	1.80	bcd	1.92	a	1.88	
C3	1.87	abcd	1.87	a	1.94	
C4	2.01	a	1.94	a	1.89	
C5	1.74	bcd	1.79	abc	1.79	
S1	1.88	abc	1.77	abc	1.78	
S2	1.81	bcd	1.62	bcd	1.66	
S3	1.76	bcd	1.60	cd	1.83	
S4	1.75	bcd	1.65	bcd	1.74	
S5	1.81	bcd	1.60	cd	1.84	
Ss	1.75	bcd	1.60	cd	1.72	
Sr	1.67	d	1.42	d	1.64	
Nematicide						
Not applied	1.83		1.85	A	1.85	A
Applied	1.80		1.61	B	1.73	B
ANOVA (*F* values)						
Rotation (R)	1.93	*	3.47	**	1.22	
Year (Y) x R	2.19	*	0.62		0.76	
Nematicide (N)	1.27		36.04	**	7.24	**
Y x N	1.42		0.28		6.13	*
R x N	0.54		1.64		0.62	
Y x R x N	1.39		1.28		1.12	

† Vi, Vm, and Vf are mean values prior to planting, at midseason (64 and 45 days after planting in 2013 & 2014), and at harvest respectively.
‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor (nematicide or rotation).
• Cn and Cc are continuous corn recently (2010-2014) with non-Bt and Bt cultivars respectively; C1 through C5 are 1st to 5th yr corn after 5 yr of soybean; S1 through S5 are 1st to 5th yr soybean following 5 yr of corn; Ss and Sr are continuous soybean recently (2010-2014) with SCN-susceptible and resistant cultivars respectively. All soybeans, except Sr, were SCN-susceptible.
* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively

3.2.4 Omnivore and predator populations

Omnivore and predator populations were small at site, averaging 11 and 1 nematode/100 cm^3 soil respectively across all plots and seasons. In fall, omnivore population was significantly ($P \leq 0.01$) decreased by nematicide application (5 and 12 omnivores/100 cm^3 soil, in nematicide and non-nematicide treatments, respectively) in fall (data not shown). Predator population was significantly ($P \leq 0.05$) decreased by

nematicide application compared to without nematicide application (1 and 2 predators/100 cm^3 soil) before planting (data not shown). Neither omnivore nor predator populations were significantly affected by crop sequence ($P > 0.05$).

3.2.5 Total nematode population

Total nematode population densities were significantly decreased by nematicide applications in all three seasons compared to without nematicide application (Table 3.8). There were also significant crop sequence by nematicide interactions in all three seasons (Table 3.8). However, in spring and midseason, there were very few significant differences among crop sequences either with nematicide or without nematicide application (Table 3.7). In fall, there were significant crop sequence effects with nematicide and without nematicide application (Table 3.7). With nematicide application, population densities were significantly greater in extended soybean monoculture than some corn sequences. In contrast, without nematicide application, population densities were significantly smaller in extended soybean monoculture and significantly greater in extended corn monoculture.

3.3 Diversity indices

The Shannon-Weaver Diversity Index was significantly decreased by nematicide applications in midseason and fall (Table 3.9). There was significant year by crop sequence interaction before planting (Table 3.9) with significant ($P < 0.05$) crop sequence effects in 2013 but not 2014 (data not shown). Before planting in 2013, diversity was significantly smaller in Sr than any other sequence while diversity was significantly greater in long-term corn monoculture (Cc and Cn) and in C4--following 3 years corn--compared to all sequences following soybean. There were significant crop sequence effects in midseason and diversity was significantly greater in corn than soybean for most sequences (Table 3.9) .

3.4 Maturity indices

3.4.1 Maturity index (MI)

The maturity index was significantly decreased by nematicide application in all three seasons (Table 3.10). The maturity index was also significantly affected by crop sequence in all three seasons (Table 3.10) and, across seasons, was significantly greater in, or, before planting, following corn than soybean--excluding the first year in each crop. Before planting, the maturity index was not significantly different across sequences following soybean. Similarly, in midseason and fall the maturity index was

not significantly different across soybean sequences except 1st-year soybean. In spring, amoung sequences following corn, the maturity index was significantly smaller following 1st-year corn but not significantly different following other corn sequences. Similarly, in midseason values were significantly smaller under C1 than C3, Cc, or Cn; but similar among other corn sequences. In fall, the maturity index increased significantly as years in corn increased from 1 to 3 years, but was similar amoung other corn sequences.

Table 3.10. The maturity index as influenced by crop sequences and nematicide application for 2013 and 2014 combined.

	Vi†	‡	Vm		Vf	
Rotation•						
Cn	1.49	ab	1.49	a	1.72	a
Cc	1.47	ab	1.46	ab	1.76	a
C1	1.27	de	1.29	cde	1.53	c
C2	1.36	cd	1.42	abc	1.64	b
C3	1.41	bc	1.49	a	1.74	a
C4	1.55	a	1.43	abc	1.77	a
C5	1.47	ab	1.33	bcde	1.71	ab
S1	1.49	ab	1.40	abcd	1.55	c
S2	1.29	de	1.26	de	1.35	de
S3	1.26	e	1.26	de	1.32	e
S4	1.26	de	1.25	e	1.33	de
S5	1.29	de	1.26	e	1.41	d
Ss	1.32	cde	1.26	de	1.34	de
Sr	1.26	de	1.20	e	1.38	de
Nematicide						
Not applied	1.40	A	1.39	A	1.57	A
Applied	1.34	B	1.30	B	1.51	B
ANOVA (*F* values)						
Rotation (R)	9.19	**	3.64	**	39.99	**
Year (Y) x R	1.72		0.53		1.36	
Nematicide (N)	9.44	**	25.67	**	8.45	**
Y x N	0.00		1.82		0.73	
R x N	0.91		1.09		0.91	
Y x R x N	0.71		0.97		1.04	

† Vi, Vm, and Vf are mean values prior to planting, at midseason (64 and 45 days after planting in 2013 & 2014), and at harvest respectively.
‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor (nematicide or rotation).
• Cn and Cc are continuous corn recently (2010-2014) with non-Bt and Bt cultivars respectively; C1 through C5 are 1st to 5th yr corn after 5 yr of soybean; S1 through S5 are 1st to 5th yr soybean following 5 yr of corn; Ss and Sr are continuous soybean recently (2010-2014) with SCN-susceptible and resistant cultivars respectively. All soybeans, except Sr, were SCN-susceptible.
* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively

Table 3.11. MI25 as influenced by crop sequences and nematicide application for 2013 and 2014 combined.

	Vi†	‡	Vm		Vf	
Rotation•						
Cn	2.15		2.15	cd	2.03	
Cc	2.05		2.13	cd	2.05	
C1	2.13		2.27	abcd	2.03	
C2	2.11		2.15	bcd	2.05	
C3	2.11		2.12	d	2.03	
C4	2.17		2.15	cd	2.05	
C5	2.13		2.26	abcd	2.07	
S1	2.09		2.33	a	2.04	
S2	2.09		2.23	abcd	2.07	
S3	2.14		2.32	ab	2.10	
S4	2.13		2.29	abc	2.07	
S5	2.11		2.27	abcd	2.04	
Ss	2.14		2.32	ab	2.10	
Sr	2.05		2.11	d	2.13	
Nematicide						
Not applied	2.13		2.25		2.08	A
Applied	2.10		2.20		2.04	B
ANOVA (*F* values)						
Rotation (R)	1.06		2.05	*	1.04	
Year (Y) x R	1.40		1.39		0.74	
Nematicide (N)	3.58		2.65		7.00	**
Y x N	4.45	*	0.65		0.42	
R x N	1.13		2.01	*	0.87	
Y x R x N	1.29		2.09	*	1.14	

† Vi, Vm, and Vf are mean values prior to planting, at midseason (64 and 45 days after planting in 2013 & 2014), and at harvest respectively.

‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor (nematicide or rotation).

• Cn and Cc are continuous corn recently (2010-2014) with non-Bt and Bt cultivars respectively; C1 through C5 are 1st to 5th yr corn after 5 yr of soybean; S1 through S5 are 1st to 5th yr soybean following 5 yr of corn; Ss and Sr are continuous soybean recently (2010-2014) with SCN-susceptible and resistant cultivars respectively. All soybeans, except Sr, were SCN-susceptible.

* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively

Table 3.12. Effects of crop sequences on nematode community indices with and without nematicide application at midseason for 2013 and 2014 combined.

	PPI		MI25		FBPP	
	Nematicide	No Nematicide	Nematicide	No Nematicide	Nematicide	No Nematicide
Rotation•	‡					
Cn	2.40 ef	2.58 abcde	2.18	2.12 cd	1.52 d	0.53 e
Cc	2.53 bcde	2.45 de	2.08	2.18 bcd	1.42 d	0.64 e
C1	2.79 a	2.74 a	2.18	2.35 abc	2.87 bcd	4.41 a
C2	2.44 cdef	2.39 ef	2.24	2.06 d	3.72 bc	1.56 cd
C3	2.36 ef	2.53 bcde	2.09	2.15 cd	3.36 bcd	0.87 de
C4	2.41 def	2.54 bcde	2.16	2.15 cd	1.44 d	0.62 e
C5	2.44 cdef	2.54 bcde	2.27	2.25 abcd	1.92 cd	0.53 e
S1	2.34 f	2.49 cde	2.10	2.56 a	1.54 d	0.70 e
S2	2.51 bcdef	2.61 abcd	2.17	2.29 abcd	4.13 b	1.74 bc
S3	2.60 abcd	2.48 cde	2.37	2.27 abcd	3.78 b	2.11 bc
S4	2.73 a	2.52 cde	2.29	2.30 abc	4.08 b	1.73 cd
S5	2.62 abc	2.71 ab	2.31	2.23 abcd	5.91 b	2.41 bc
Ss	2.70 ab	2.66 abc	2.26	2.38 ab	3.63 bc	2.74 ab
Sr	2.42 def	2.22 f	2.06	2.16 bcd	12.53 a	3.90 a
ANOVA (*F* values)						
Rotation (R)	4.47 **	3.40 **	1.42	1.84 *	6.65 **	11.3 **

	BI		CI	
	Nematicide	No Nematicide	Nematicide	No Nematicide
Rotation•				
Cn	9.5 abc	16.5 a	6.3 abc	12.8 a
Cc	12.0 ab	13.7 abc	10.3 abc	8.8 abc
C1	5.2 cde	6.9 de	1.8 d	3.9 bcd
C2	7.0 abcd	16.6 a	4.8 bc	13.4 a
C3	13.1 a	15.5 ab	9.4 ab	12.8 a
C4	10.9 a	11.6 abcd	9.4 a	9.0 ab
C5	7.0 abcd	6.9 de	4.7 c	5.6 bcd
S1	12.3 a	9.2 bcde	7.7 abc	5.9 bcd
S2	4.3 de	6.4 de	2.0 d	3.3 cd
S3	3.8 de	7.3 cde	1.4 d	3.0 d
S4	3.8 de	6.1 de	1.3 d	2.5 d
S5	3.9 e	8.6 cde	1.0 d	3.9 bcd
Ss	5.4 bcde	5.1 e	1.8 d	3.4 cd
Sr	4.0 de	6.4 de	1.9 d	3.7 bcd
ANOVA (*F* values)				
Rotation (R)	3.89 **	3.19 **	8.74 **	4.33 **

‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values.

• Cn and Cc are continuous corn recently (2010-2014) with non-Bt and Bt cultivars respectively; C1 through C5 are 1st to 5th yr corn after 5 yr of soybean; S1 through S5 are 1st to 5th yr soybean following 5 yr of corn; Ss and Sr are continuous soybean recently (2010-2014) with susceptible and resistant cultivars respectively.

* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively

3.4.2 MI25

MI25 was significantly decreased under nematicide application in fall (Table 3.11). In spring, there were significant year by nematicide interactions with MI25 decreased by nematicide application in 2014 ($P < 0.05$, values of 2.10 and 2.16), but not affected by nematicide application in 2013 ($P > 0.05$). There were significant crop sequence effects only in midseason and only for the treatment without nematicide application (Table 3.12). In midseason, without nematicide, MI25 was similar among most sequences, but significantly decreased in extended corn monoculture (3 or more years in corn) than in some soybean sequences.

3.4.3 Plant parasite index (PPI)

There were significant nematicide by year interactions for the plant parasite index in midseason and fall (Table 3.13). In midseason, nematicide significantly decreased ($P \leq 0.01$) the plant parasite index from 2.59 to 2.46 in 2013 compared to without nematicide, but increased it from 2.48 to 2.58 in 2014 (data not shown). In fall, nematicide significantly decreased ($P \leq 0.05$) values from 2.62 to 2.41 only in 2013.

There was significant nematicide by crop sequence interaction in midseason (Table 3.13) with significant crop sequence effects both with nematicide and without nematicide application (Table 3.12). Under nematicide application, the plant parasite index was significantly greater in extended soybean monoculture (4 or more years) than some corn sequences. Without nematicide application, the plant parasite index was not significantly different among most sequences. Under either nematicide treatment at midseason, the plant parasite index was significantly smaller under Sr than most other crop sequences.

Under combined nematicide treatments in spring and fall, there were significant crop sequence effects and values were also significantly smaller under SCN-resistant soybean monoculture than most other crop sequences (Table 3.13). Before planting, the plant parasite index was significantly greater following 4 or more years in soybean monoculture than sequences in less than 3 years of soybean and some corn sequences. Similarly, in fall, the plant parasite index was significantly greater in 4 or more years of soybean than most corn sequences or 1st-year soybean.

Table 3.13. The plant parasite index as influenced by crop sequences and nematicide application for 2013 and 2014 combined.

	Vi†	‡	Vm		Vf	
Rotation•						
Cn	2.76	abcd	2.49	ef	2.48	def
Cc	2.66	bcde	2.49	def	2.37	fg
C1	2.85	a	2.77	a	2.70	a
C2	2.69	abcde	2.42	efg	2.47	def
C3	2.62	def	2.45	efg	2.44	ef
C4	2.57	ef	2.48	ef	2.52	cde
C5	2.63	cde	2.49	def	2.47	def
S1	2.70	abcde	2.41	fg	2.38	fg
S2	2.47	f	2.56	bcde	2.57	bcd
S3	2.59	ef	2.54	cdef	2.53	cde
S4	2.62	def	2.63	abcd	2.69	ab
S5	2.79	ab	2.67	abc	2.66	ab
Ss	2.77	abc	2.68	ab	2.59	abc
Sr	2.24	g	2.32	g	2.31	g
Nematicide						
Not applied	2.65		2.54		2.59	A
Applied	2.64		2.52		2.45	B
ANOVA (*F* values)						
Rotation (R)	7.00	**	5.74	**	7.96	**
Year (Y) x R	0.85		1.82		1.52	
Nematicide (N)	0.12		0.66		36.49	**
Y x N	0.31		27.03	**	10.06	**
R x N	1.69		2.69	**	1.39	
Y x R x N	1.11		0.84		0.42	

† Vi, Vm, and Vf are mean values prior to planting, at midseason (64 and 45 days after planting in 2013 & 2014), and at harvest respectively.

‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor (nematicide or rotation).

• Cn and Cc are continuous corn recently (2010-2014) with non-Bt and Bt cultivars respectively; C1 through C5 are 1st to 5th yr corn after 5 yr of soybean; S1 through S5 are 1st to 5th yr soybean following 5 yr of corn; Ss and Sr are continuous soybean recently (2010-2014) with SCN-susceptible and resistant cultivars respectively. All soybeans, except Sr, were SCN-susceptible.

* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively

3.5 Food web indices

3.5.1 Enrichment index (EI)

The enrichment index was significantly increased by nematicide applications compared to without nematicide application and affected by crop sequence in all three seasons (Table 3.14). Across seasons, the enrichment index was significantly greater under soybean than corn for most sequences (Table 3.14). Before planting, the

enrichment index was not significantly different among sequences following soybean. In midseason and fall, values were significantly smaller in 1st-year soybean than most other soybean sequences, but were not significantly different among other soybean sequences. Before planting, among sequences following corn, values were generally not significantly different. Similarly, in midseason, values were significantly greater in 1st-year corn than most other corn sequences, but not significantly different among other corn sequences. In fall, values increased significantly from 1st to 2nd to 3rd year corn, but were not significantly different among other corn sequences.

Table 3.14. The enrichment index as influenced by crop sequences and nematicide application for 2013 and 2014 combined.

	Vi†	‡	Vm		Vf	
Rotation•						
Cn	85	de	86	d	69	fg
Cc	84	e	86	d	68	fg
C1	92	ab	94	ab	80	c
C2	90	abc	88	cd	75	de
C3	88	bcd	84	d	69	fg
C4	83	e	88	cd	67	g
C5	87	cde	93	abc	72	ef
S1	84	e	89	bcd	79	cd
S2	92	a	94	a	88	ab
S3	93	a	94	a	91	a
S4	93	a	95	a	90	a
S5	92	ab	94	ab	86	b
Ss	91	ab	95	a	89	ab
Sr	92	ab	95	a	89	ab
Nematicide						
Not applied	88	B	90	B	78	B
Applied	90	A	92	A	80	A
ANOVA (*F* values)						
Rotation (R)	7.13	**	4.61	**	37.79	**
Year (Y) x R	1.04		0.22		1.43	
Nematicide (N)	4.85	*	13.95	**	3.83	*
Y x N	0.86		1.15		0.57	
R x N	0.92		1.61		0.88	
Y x R x N	0.48		0.61		1.16	

† Vi, Vm, and Vf are mean values prior to planting, at midseason (64 and 45 days after planting in 2013 & 2014), and at harvest respectively.

‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor (nematicide or rotation).

• Cn and Cc are continuous corn recently (2010-2014) with non-Bt and Bt cultivars respectively; C1 through C5 are 1st to 5th yr corn after 5 yr of soybean; S1 through S5 are 1st to 5th yr soybean following 5 yr of corn; Ss and Sr are continuous soybean recently (2010-2014) with SCN-susceptible and resistant cultivars respectively. All soybeans, except Sr, were SCN-susceptible.

* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively

Table 3.15. The basal index as influenced by crop sequences and nematicide application for 2013 and 2014 combined.

	Vi†	‡	Vm		Vf	
Rotation•						
Cn	14.1	abc	13.0	ab	30.4	a
Cc	15.9	a	12.8	ab	31.3	a
C1	7.8	de	6.1	cd	20.1	d
C2	10.3	cde	11.8	ab	24.6	bc
C3	11.6	bcd	14.3	a	30.3	a
C4	15.9	a	11.2	ab	31.8	a
C5	12.6	abc	7.0	bcd	27.3	ab
S1	15.2	ab	10.7	abc	20.3	cd
S2	7.7	e	5.4	cd	11.2	ef
S3	6.7	e	5.6	cd	9.0	f
S4	6.8	e	5.0	cd	10.0	f
S5	7.9	de	6.2	d	13.9	e
Ss	8.4	de	5.3	cd	11.1	ef
Sr	8.2	de	5.2	d	10.9	ef
Nematicide						
Not applied	11.5	A	9.8	A	21.0	
Applied	9.9	B	7.4	B	19.5	
ANOVA (*F* values)						
Rotation (R)	6.84	**	5.19	**	35.64	**
Year (Y) x R	1.03		0.42		1.22	
Nematicide (N)	4.01	*	14.16	**	2.89	
Y x N	1.50		0.04		0.63	
R x N	0.93		1.96	*	0.93	
Y x R x N	0.53		1.22		1.04	

† Vi, Vm, and Vf are mean values prior to planting, at midseason (64 and 45 days after planting in 2013 & 2014), and at harvest respectively.
‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor (nematicide or rotation).
• Cn and Cc are continuous corn recently (2010-2014) with non-Bt and Bt cultivars respectively; C1 through C5 are 1st to 5th yr corn after 5 yr of soybean; S1 through S5 are 1st to 5th yr soybean following 5 yr of corn; Ss and Sr are continuous soybean recently (2010-2014) with SCN-susceptible and resistant cultivars respectively. All soybeans, except Sr, were SCN-susceptible.
* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively

3.5.2 Basal index (BI)

In both spring and midseason, the basal index was significantly decreased by nematicide applications (Table 3.15). In midseason, there was significant crop sequence by nematicide interaction (Table 3.15) with significant crop sequence effects both with nematicide and without nematicide application (Table 3.12). The basal index was significantly greater in many corn than many soybean sequences although more

contrasts were significant for treatment with nematicide than treatment without nematicide (Table 3.12).

Significant crop sequence effects were also observed in spring and fall with combined nematicide treatments (Table 3.15). Before planting, the basal index was significantly greater following sequences in corn 3 or more years than following most soybean sequences. Similarly, in fall, values were significantly greater in any corn sequence than any sequence in soybean 2 or more years. Before planting, values were significantly greater for most sequences following 3 or more years in corn than following 2 or few years in corn. Similarly, in fall, values significantly increased as years in corn increased, up to 3 years in corn, but values in 3 or more years in corn were not significantly different. Additionally, values were significantly greater in, for fall, or following, before planting, 1st-year soybean than any other length of soybean.

3.5.3 Structure index (SI)

The structure index was significantly decreased by nematicide application in spring and fall (Table 3.16). There was significant crop sequence by year interaction before planting (Table 3.16). There were no crop sequence effects in 2014 ($P > 0.05$), but in 2013, the structure index was significantly ($P < 0.05$) greater under sequences following 5 or more years of corn monoculture and smaller in Sr than most sequences (data not shown).

3.5.4 Channel index (CI)

The channel index was significantly decreased by nematicide application in spring and midseason (Table 3.17). There were significant crop sequence by nematicide interactions in midseason (Table 3.17) with significant crop sequence effects both with nematicide and without nematicide application (Table 3.12). The channel index was significantly greater in most corn than most soybean sequences, although more contrasts were significant in treatment with nematicide than treatment without nematicide application. Without nematicide, values were not significantly different among soybean sequences while with nematicide values were significantly greater in 1st-year soybean than other soybean sequences, but similar among other soybean sequences. For both treatments, values were significantly smaller in 1st and 5th year corn than most other corn sequences.

Table 3.16. The structure index as influenced by crop sequences and nematicide application for 2013 and 2014 combined.

	Vi†	‡	Vm	Vf	
Rotation•					
Cn	20.7	ab	19.4	5.3	
Cc	8.0	cd	19.2	8.5	
C1	19.1	abc	31.6	5.3	
C2	14.9	bcd	20.4	7.8	
C3	17.2	ab	17.9	5.8	
C4	24.6	a	22.5	7.8	
C5	20.6	ab	32.2	9.8	
S1	13.7	abc	29.8	7.4	
S2	13.4	bc	29.9	10.8	
S3	19.6	ab	36.8	13.4	
S4	18.7	ab	34.4	10.7	
S5	15.6	bcd	29.6	7.7	
Ss	19.8	abc	38.2	12.7	
Sr	6.2	d	15.9	17.0	
Nematicide					
Not applied	18.8	A	29.6	11.5	A
Applied	14.7	B	24.9	6.8	B
ANOVA (*F* values)					
Rotation (R)	2.43	**	1.65	0.32	
Year (Y) x R	1.85	*	0.70	0.49	
Nematicide (N)	6.65	*	3.05	8.71	**
Y x N	2.79		0.03	0.82	
R x N	0.87		1.33	1.53	
Y x R x N	0.88		1.07	1.22	

† Vi, Vm, and Vf are mean values prior to planting, at midseason, and at harvest .
‡ Different letters in the same column indicate significant difference (Fischer's LSD, *P*≤0.05) between transformed mean values within the same factor (nematicide or rotation).
• Cn and Cc are continuous corn recently (2010-2014) with non-Bt and Bt cultivars respectively; C1 through C5 are 1st to 5th yr corn after 5 yr of soybean; S1 through S5 are 1st to 5th yr soybean following 5 yr of corn; Ss and Sr are continuous soybean recently (2010-2014) with SCN-susceptible and resistant cultivars respectively. All soybeans, except Sr, were SCN-susceptible.
* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively

In spring and fall, for combined nematicide treatments, there were significant crop sequence effects on the channel index (Table 3.17). Before planting, values were not significantly different following soybean sequences, but significantly greater following corn than soybean sequences (Table 3.17). Similarly, in fall, values were significantly greater in corn than soybean sequences, excluding 1st year sequences. In fall, values were also significantly smaller in first-year soybean than other soybean sequences, but not significantly different among other soybean sequences. Before planting, values were

significantly smaller following first-year corn than other corn sequences, but similar among other corn sequences. In fall, the channel index significantly increased as years in corn increased for the first 3 years in corn, but values were not significantly different among other corn sequences.

3.5.5 FBPP

FBPP, fungivore and bacterivore divided by herbivore population densities, was significantly increased by nematicide application in all three seasons (Table 3.18). There were was significant crop sequence by nematicide interactions in midseason (Table 3.18) with significant crop sequences in both treatment with nematicide and treatment without nematicide application (Table 3.12). FBPP was significantly greater in 2 or more years of soybean monoculture than 1st-year soybean and most sequences in 4 or more years of corn for both treatment with nematicide application and treatment without nematicide applicaton. Values were significantly greater under SCN-resistant soybean than most other sequences under either nematicide treatment. In treatment with nematicide application, values were not significantly different among corn sequences while without nematicide values significantly increased with increases in length of corn monoculture for some contrasts.

Similarly, in spring and fall, for combined nematicide treatments, FBPP significantly increased with increases in length of corn monoculture for some contrasts (Table 3.18). Before planting, FBPP values were generally greater in sequences following soybean than following 3 or more years of corn (Table 3.18). Similarly, in fall, values were significantly greater in sequences in 2 or more years of soybean than in corn sequences. Before planting, values were generally not different following SCN-susceptible soybean, but greater in SCN-resistant soybean than most sequences. In fall, values were significantly smaller in S1 and larger in Ss compared to most soybean sequences. In both spring and fall, values significantly increased with increases in length of corn monoculture for some contrasts.

Table 3.17. The channel index as influenced by crop sequences and nematicide application for 2013 and 2014 combined.

	Vi†	‡	Vm		Vf	
Rotation•						
Cn	9.2	bc	9.5	ab	31.1	abc
Cc	11.9	ab	9.5	abc	33.0	ab
C1	2.9	d	2.9	d	14.5	d
C2	6.1	c	9.1	abc	24.9	c
C3	9.2	ab	11.1	a	34.1	a
C4	12.9	a	9.2	ab	32.2	ab
C5	8.9	b	5.1	c	25.9	bc
S1	9.7	ab	6.8	bc	11.0	d
S2	3.5	d	2.6	d	6.6	e
S3	2.2	d	2.2	d	3.5	e
S4	2.5	d	1.9	d	3.2	e
S5	3.0	d	2.5	d	4.8	e
Ss	3.0	d	2.6	d	4.7	e
Sr	3.2	d	2.8	d	5.3	e
Nematicide						
Not applied	7.1	A	6.6	A	16.8	
Applied	5.7	B	4.6	B	17.0	
ANOVA (*F* values)						
Rotation (R)	18.37	**	9.89	**	52.90	**
Year (Y) x R	1.08		0.36		1.21	
Nematicide (N)	5.59	*	23.64	**	0.56	
Y x N	0.04		2.45		0.43	
R x N	0.38		1.84	*	1.63	
Y x R x N	0.82		0.43		0.66	

† Vi, Vm, and Vf are mean values prior to planting, at midseason (64 and 45 days after planting in 2013 & 2014), and at harvest respectively.

‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor (nematicide or rotation).

• Cn and Cc are continuous corn recently (2010-2014) with non-Bt and Bt cultivars respectively; C1 through C5 are 1st to 5th yr corn after 5 yr of soybean; S1 through S5 are 1st to 5th yr soybean following 5 yr of corn; Ss and Sr are continuous soybean recently (2010-2014) with SCN-susceptible and resistant cultivars respectively. All soybeans, except Sr, were SCN-susceptible.

* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively

Table 3.18. FBPP as influenced by crop sequences and nematicide application for 2013 and 2014 combined.

	Vi†	‡	Vm		Vf	
Rotation•						
Cn	0.75	e	1.03	e	1.45	ef
Cc	1.00	e	1.03	e	1.27	efg
C1	2.43	bc	3.64	b	2.36	cd
C2	2.57	bc	2.64	bc	2.64	c
C3	2.71	bc	2.12	cd	2.05	de
C4	1.31	de	1.03	e	1.01	fg
C5	1.08	e	1.22	de	0.87	g
S1	0.90	e	1.12	de	1.58	e
S2	2.70	bc	2.93	b	4.51	b
S3	3.34	b	2.95	b	4.87	b
S4	2.93	bc	2.91	b	5.96	ab
S5	1.91	cd	4.16	b	5.04	b
Ss	3.27	b	3.19	b	6.60	a
Sr	9.82	a	8.21	a	4.95	b
Nematicide						
Not applied	2.00	B	1.70	B	1.62	B
Applied	2.98	A	3.56	A	4.80	A
ANOVA (*F* values)						
Rotation (R)	19.40	**	15.16	**	34.23	**
Year (Y) x R	0.95		0.66		1.68	
Nematicide (N)	40.91	**	74.68	**	211.42	**
Y x N	1.32		0.18		9.55	**
R x N	1.62		1.86	*	1.14	
Y x R x N	1.48		0.41		1.08	

† Vi, Vm, and Vf are mean values prior to planting, at midseason (64 and 45 days after planting in 2013 & 2014), and at harvest respectively.

‡ Different letters in the same column indicate significant difference (Fischer's LSD, $P \leq 0.05$) between transformed mean values within the same factor (nematicide or rotation).

• Cn and Cc are continuous corn recently (2010-2014) with non-Bt and Bt cultivars respectively; C1 through C5 are 1st to 5th yr corn after 5 yr of soybean; S1 through S5 are 1st to 5th yr soybean following 5 yr of corn; Ss and Sr are continuous soybean recently (2010-2014) with SCN-susceptible and resistant cultivars respectively. All soybeans, except Sr, were SCN-susceptible.

* and ** represent significant effects at $P \leq 0.05$ and $P \leq 0.01$ respectively

4. Discussion

Nematicide was consistently effective against its target, herbivores, and decreased nematode population for nearly a year following nematicide application. This

long-lasting effect may have been enhanced because application was repeated yearly. However, nematicide also reduced populations of non-target, beneficial nematodes including bacterivores, fungivores, omnivores and predators in various seasons. The loss of the ecological services provided by these nematodes and the organisms they are indicative of contributes to the cost of nematicide application, although this loss is not easily quantified (Anderson et al., 1983; Bongers, 1990; Ferris et al., 1998; Chen and Ferris, 1999; Ferris et al., 2001).

Prior information on the impact of aldicarb nematicide application on the nematode community is limited, but in another study aldicarb application reduced populations of free-living nematodes in most fields it was applied (Smolik, 1983). Aldicarb is not currently in production, so its impacts in the present study serve as a general example of the effects of nematicide application rather than as a case study for this particular nematicide. In other studies, application of other granular nematicides also reduced populations of free-living nematodes, particularly bacterivores and fungivores (Pen-Mouratov and Steinberger, 2005; Chelinho et al., 2011; Wada et al., 2011). Fumigant nematicides, which are applied across the entire soil surface and target a broad spectrum of organisms, affected most trophic groups (Wang et al., 2006; Sanchez-Moreno et al., 2010; Timper et al., 2012).

Bacterivore and fungivore populations were impacted for shorter duration during the present study than herbivores, a trend observed with application of some pesticides (Wang et al., 2006; Timper et al., 2012). This suggests bacterivores and fungivores were more resilient than herbivores. The release of organic matter from the death of other organisms due to nematicide application may have stimulated microbial growth increasing food resources for bacterivores and fungivores and helping counteract initial decrease in fungivore and bacterivore populations from nematicide application.

Diversity was decreased by nematicide application through one growing season and is similar to other results with granular nematicide (Pen-Mouratov and Steinberger, 2005) and fumigants (Ettema and Bongers, 1993; Wang et al., 2006; Sanchez-Moreno et al., 2010). Decreased maturity and structure indices with nematicide application suggest nematicide application disturbed the soil food web a full year after application. Similarly, in other studies, both granular nematicides (Pen-Mouratov and Steinberger, 2005) and fumigants (Wang et al., 2006; Sanchez-Moreno et al., 2010; Timper et al., 2012) reduced soil community maturity. MI25 was not affected by nematicide

application consistently, suggesting disturbance was based mostly on enrichment which may reflect having a community predominantly of enrichment opportunists.

Based on the enrichment index, nematicide application enriched the soil ecosystem, which is consistent with an influx of resources from decaying organisms. Based on the basal index, nematicide application shifted the ecosystem away from a basal trajectory and toward an enrichment trajectory. While most other studies did not examine enrichment, carbofuran granular nematicide (Chelinho et al., 2011) and the fumigant 1,3-dichloropropene (1,3-D) enriched the nematode community (Sanchez-Moreno et al., 2010). However, 1,3-D in combination with aldicarb granular nematicide did not affect soil food web enrichment in a separate study (Timper et al., 2012).

Based on decreases in channel index with nematicide application, nematicide application shifted decomposition pathways toward bacterial rather than fungal channels. This is consistent with enrichment of the ecosystem under nematicide application and with the results of other studies (Wang et al., 2006; Timper et al., 2012). Similarly, nematicide application shifted FBPP ratio toward free-living nematodes again showing nematicide application was more effective against herbivores than free-living nematodes.

In the initial years in a particular crop, the number of years varied by population or indicator, most nematode populations and indices shifted increasing values in one crop generally corresponding with decreasing values in the other crop. This lead to different nematode community characteristics between the two crops particularly in monoculture. For most nematode indicators, and thus aspects of soil ecology, after a certain number of years in a particular crop, which varied by indicator, values stopped changing with increasing years in monoculture or the rate of change was dramatically reduced, although seasonal variations still occurred. This suggests the corresponding aspect of the soil community had reached an equilibrium status for that particular crop within the given agricultural environment and further increases in monoculture would not substantially shift that aspect of the soil community. These states of equilibrium did not equate to an advanced stage of ecological succession as the site was intensively managed and every cropping sequence was classified as a disturbed system (enrichment index greater than 50, structure index less than 50) according to the faunal profile (Ferris et al., 2001). Other long-term crop sequence experiments that examined

the nematode community did not have comparable designs to this study, so they cannot be used to confirm these trends (Rahman et al., 2007; Djigal et al., 2012).

The extent of differences between cropping systems varied for different nematode indicators of soil ecology and fluctuated by season, but corn and soybean cropping systems had distinct characteristics. In particular, conditions were better for herbivore development in corn compared to soybean monoculture based on differences in herbivore populations. While corn was better than soybean for fungivore development, soybean was better than corn for bacterivore development. As expected given these trends in bacterivore and fungivore populations, corn monoculture promoted fungal rather than bacterial-based decomposition pathways compared to soybean monoculture based on the channel index. These trends suggest corn systems were more conducive to fungal growth which is associated with a more stable or structured ecosystem (Ferris et al., 2001). In contrast, soybean systems were more conducive to bacterial growth and had a more highly enriched food web. Since bacteria have a lower C:N ratio than fungi (Woods et al., 1982; Anderson et al., 1983; Chen and Ferris, 1999), these trends also suggest system inputs had a smaller C:N ratio under soybean than corn as confirmed elsewhere (Salvator and Sabbe, 1995; Halvorson and Schlegel, 2012). Corn residue C:N ratio is also greater following corn than soybean (Gentry et al., 2001) which may have accelerated the shift toward fungivores under corn monoculture. Additionally, corn takes up more nitrogen from the soil than soybean on a per hectare basis (Halvorson and Schlegel, 2012) resulting in nitrogen immobilization (Salvator and Sabbe, 1995), which may also contribute to greater C:N ratio in the soil under corn than soybean. In another study, adding inputs with greater C:N ratio also increased fungivore and decreased bacterivore population compared to adding inputs with smaller C:N ratio (Ferris et al., 1996).

Differences in the basal and enrichment indices between cropping systems were related to greater population of enrichment-opportunist bacterivores under soybean than corn systems and suggested soybean monoculture created more enriched conditions than corn monoculture (Ferris et al., 2001). These trends in enrichment, fungivore populations, and bacterivore populations suggest nutrient mineralization by microorganisms may play a role in plant growth benefits from crop rotation, particularly for corn. Bacterivores, fungivores, and the microbial food sources these nematodes are indicators of are known to mineralize nutrients with bacteria and bacterivores having a

larger contribution (Woods et al., 1982; Rosswall and Paustian, 1984; Ferris et al., 1998; Chen and Ferris, 1999; Holtkamp et al., 2011). This suggests nutrient mineralization may have been increased under soybean compared to corn production since bacterivore populations were also increased in soybean. In turn, increased nutrient mineralization following soybean could play a role in increasing corn yield in corn-soybean crop rotation. Other studies have suggested increased nutrient mineralization following soybean compared with corn contributes to benefits of corn-soybean rotation for corn (Green and Blackmer, 1995; Gentry et al., 2001).

SCN-susceptible soybean monoculture shifted balance toward free-living nematodes versus herbivores compared to corn monoculture based on FBPP (Wasilewska, 1989). In particular, this shift was a result of increased herbivore population and decreased bacterivore population, which was larger than fungivore population, under corn compared to soybean systems. Ecosystems skewed toward fungivores and bacterivores may be more healthy as they provide beneficial services to the ecosystem while herbivores are generally detrimental (Barker and Olthof, 1976; Wasilewska, 1989; Ferris et al., 1998; Chen and Ferris, 1999). Additionally, SCN-resistant soybean strongly shifted balance toward free-living nematodes compared with other systems due to control of the major plant-parasitic nematode in soybean, SCN.

Corn monoculture created a more diverse system than soybean monoculture, based on the Shannon-Weaver diversity index (Neher and Darby, 2009), although this was not consistent across seasons. Maturity index values were generally smaller in soybean than corn monoculture which reflects the relative increases in bacterivore populations, which were primarily colonizer-persister group 1 at this site (Bongers, 1990), and decreases in fungivore populations, primarily colonizer-persister group 2 (*c-p* 2) in soybean monoculture. Possible explanations for these population trends were discussed above and these differences in the maturity index suggest corn systems were more mature and less disturbed than soybean systems (Bongers, 1990). In contrast, based on the structure index, structure at the top of the soil food web was generally unaffected by crop sequence. Overall, based on small structure index values and small omnivore-predator populations, the soil food web lacked structure in these cropping systems which is similar to other agricultural systems (Sanchez-Moreno et al., 2010). Generally, MI25 was not affected by cropping system suggesting differences in maturity were driven by disturbance through enrichment since enrichment opportunists are

excluded from MI25. Since enrichment opportunists constituted a large portion of bacterivores at the site, this suggests increase of bacterivores in soybean compared to corn drove these differences in soil ecosystem maturity.

Based on the plant parasite index, SCN-susceptible soybean monoculture favored development of *c-p* 3—primarily yield-damaging herbivores--over *c-p* 2 herbivores—primarily not yield-damaging herbivores (Bongers, 1990). In contrast, corn monoculture shifted ratio toward *c-p* 2 herbivores, particularly in fall. As a ratio of between two groups, this does not necessarily reflect the difference in population of either group between the two crops. Additionally, much smaller plant parasite index values in SCN-resistant soybean than other cropping systems reflects control of the major plant-parasitic nematode in soybean at the site, SCN, which shifted balance strongly toward *c-p* 2 herbivores. Other studies have suggested the plant parasite index may be used as an indicator of disturbance (Neher and Campbell, 1996; Bongers et al., 1997; Bongers and Ferris, 1999), but results of this study suggest, in agricultural systems, it may be more appropriate to use it as an indicator of the dynamics between host-adapted and generalist herbivores.

There are few published studies on the influence of crop rotation on the nematode community, and therefore few reference points for this study. The most similar study compared corn monoculture with annual rotations involving corn, soybean, and common bean established for 25 years in Madagascar (Djigal et al., 2012). Similar to the present study, the Madagascar study found that the soil ecosystem was much different under corn monoculture than any other crop sequence, but, unlike the present study, corn monoculture was more enriched, disturbed and unstructured than other systems (Djigal et al., 2012). The differences between the results of these studies may be due to climate and soil type differences or the cover crops used in the Madagascar study. Studies involving other crop rotations also suggested that different crops drive nematode population, particularly fungivores and bacterivores, and affect the soil ecosystem in different ways (Osler et al., 2000; Rahman et al., 2007; Carter et al., 2009; Briar et al., 2012).

In the present study, nematicide application reduced differences among crop sequences for some nematode indicators including herbivore population, total nematode population, MI25, and FBPP, particularly at midseason when nematicide was more effective. In this case, increased nematode populations without nematicide application

made differences across crop sequences more distinct. In contrast, there were more differences among crop sequences with nematicide application than without nematicide application for the basal index, channel index, and the plant parasite index again generally at midseason. Decrease in basal index and channel index and increase in the plant-parasite index under soybean was intensified by nematicide application in this case.

In summary, nematicide application negatively impacted soil ecology, as indicated by the nematode community, by disturbing the soil ecosystem and reducing populations of beneficial organisms, as indicated by reductions in bacterivore and fungivores populations. Crop sequences influenced the nematode community and soil ecology. Corn systems were distinct from soybean systems particularly after initial years in crop monoculture. Soybean promoted a more enriched, disturbed ecosystem shifted toward bacterial decomposition pathways compared to corn. Corn promoted a more diverse, mature ecosystem shifted toward fungal decomposition pathways compared to soybean. These differences between corn and soybean systems suggest nutrient mineralization by nematodes and other microorganisms may play a role in the benefits of crop rotation for plant growth.

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